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Comparative leaf morphology and cuticular anatomy of *Akania bidwillii* (Akaniaceae)

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Abstract: Leaf morphology and cuticles of *Akania bidwillii* (Akaniaceae) are described and illustrated in detail for the first time and compared with leaves of *Bretschneidera sinensis* (Akaniaceae) and Tropaeolaceae. The most distinctive features of the cuticle are the discrete clusters of stomata on the abaxial surface which are both surrounded and covered by clumps of highly ornamented, coronulate papillae. The leaves were also compared to previously described fossil Akaniaceae leaves from South America. Leaf fossils from the early Miocene-aged New Zealand Foulden Maar site, from where *Akania* flowers were recently described, were also compared to the highly distinctive leaves and cuticles of *A. bidwillii*, but to date no matches have been found from there or any other New Zealand or Australian fossil sites.

Keywords: *Akania*, Akaniaceae, Brassicales, leaf cuticle, *Bretschneidera*, Tropaeolaceae

Introduction

Akaniaceae (turnipwoods) are a family of flowering trees in the order Brassicales consisting of two monotypic genera: *Akania* Hook.f. endemic to eastern Australia; and *Bretschneidera* Hemsl. in China (including Taiwan), Vietnam and India, each with a single species (Bayer & Appel 2003a; Kumar *et al.* 2017). The latter genus is sometimes placed in its own family (Lu & Boufford 2001), but was found to be sister to *Akania* in molecular studies (Gadek *et al.* 1992; Andersson & Andersson 2000), the expanded family forming a basal lineage with Tropaeolaceae, sister to the remainder of Brassicales (Cardinal-McTeague *et al.* 2016). *Akania bidwillii* (R.Hogg) Mabb. is an uncommon small rainforest understorey tree that occupies a narrow zone in coastal lowland and adjacent ranges from north-east New South Wales to south-east Queensland (Fig. 1) (Hewson 1985).

Fossils of *Akania* of Palaeocene age have been reported from South America, based on leaves with distinctive marginal tooth morphology and venation, but which lack cuticle (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007). Akaniaceae wood of Miocene age has also been described from South America (Brea *et al.* 2017). Recently, the first fossil *Akania* inflorescence and flowers with *in situ* pollen were described by Conran *et al.* (2019) from earliest Miocene lacustrine sediments at the Foulden Maar *Konservat-Lagerstätte* site near Middlemarch in southern New Zealand (45.5271° S, 170.2218° E), representing the first fossils of Akaniaceae from Australia or New Zealand. However, to date no examples of the distinctive fossil leaves have been reported from Australasia.

The leaf epidermal anatomy of *Akania* was described briefly by Solereder (1899), but not illustrated. In this paper we provide the first detailed systematic and illustrated description of the leaves and cuticles of *Akania* using both light microscopy and SEM. This will allow comparison with previous studies of its sister genus *Bretschneidera* (Qiao *et al.* 2010; Tu *et al.* 2012) and the related family Tropaeolaceae, as well as to determine if any leaves with similar epidermal features are present amongst fossils collected previously from Foulden Maar, or from other sites in New Zealand and elsewhere.

Materials and methods

Reference leaves of *Akania bidwillii* (*D.J. Mcauliffe s.n.*, AD98142330; *J.B. Williams s.n.*, NE20021; *J.G. Conran 3965*, AD, NE) were examined and comparative cuticular preparations are held in the Department of Geology Museum (OU), University of Otago, Dunedin, New Zealand. Leaf fragments for

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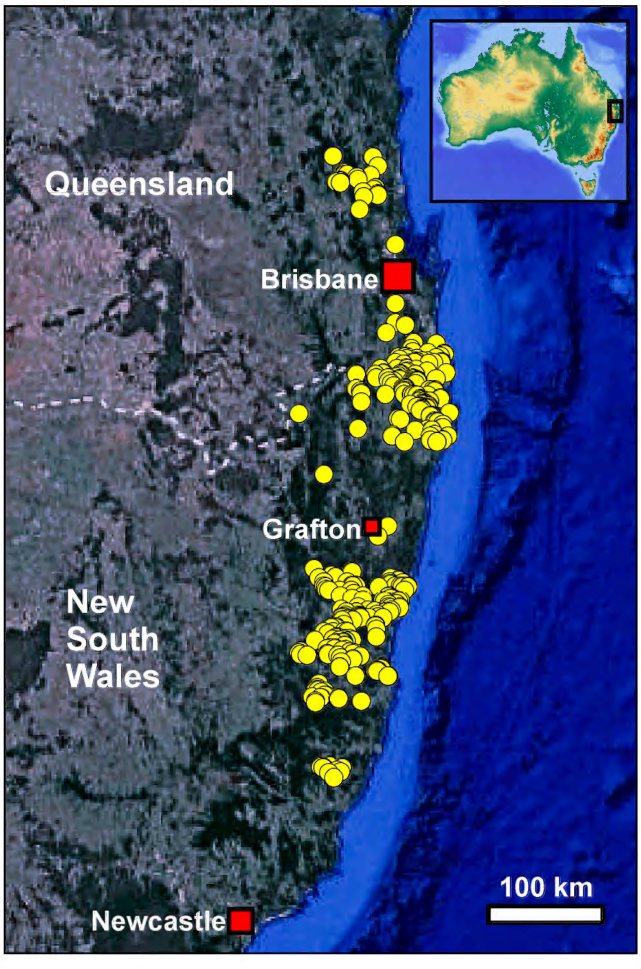


Fig. 1. Distribution map of localities for *Akania bidwillii* in eastern Australia. Source: AVH (2018).

venation were cleared by cutting small pieces from the midsection of desiccated leaves and soaking in 30% hydrogen peroxide at c. 60°C until cleared (24–48 h). The fragments were then stained in 0.5% aqueous Safranin O, differentiated to the desired transparency in 95% ethanol before slide-mounting in thymol-glycerin jelly. The cleared leaves were photographed using a Nikon D80 DSLR camera (Nikon Corporation, Tokyo, Japan). Venation features were illustrated and described following Ellis *et al.* (2009).

Akania cuticle preparation involved soaking small desiccated leaf pieces in 30% hydrogen peroxide with a few crystals of tetra-sodium pyrophosphate, warming gently and, once cleared, rinsing in distilled water. The cuticle layers were separated and debris removed with fine paintbrushes before staining with 0.1% aqueous crystal violet for c. 60 s, washing in RO water and slide mounting in thymol-glycerine jelly. Cuticles were photographed with a Leica digital camera attached to a Leica DM1000 LED microscope (Leica Microsystems GmbH, Wetzlar, Germany) using LAS software (Leica Microsystems 2015). Where appropriate, images were stacked using Picolay (Cypionka 2015). SEM of platinum-coated and stub-mounted cuticle fragments used a JEOL 6700F Field emission Scanning Electron Microscope (JEOL Ltd, Tokyo, Japan). Cuticles features were described following Wilkinson (1979). Comparative Tropaeolaceae cuticles were also prepared for *Tropaeolum majus* L. (*J.G. Conran 4006*, ADU: Adelaide University plant reference collection).

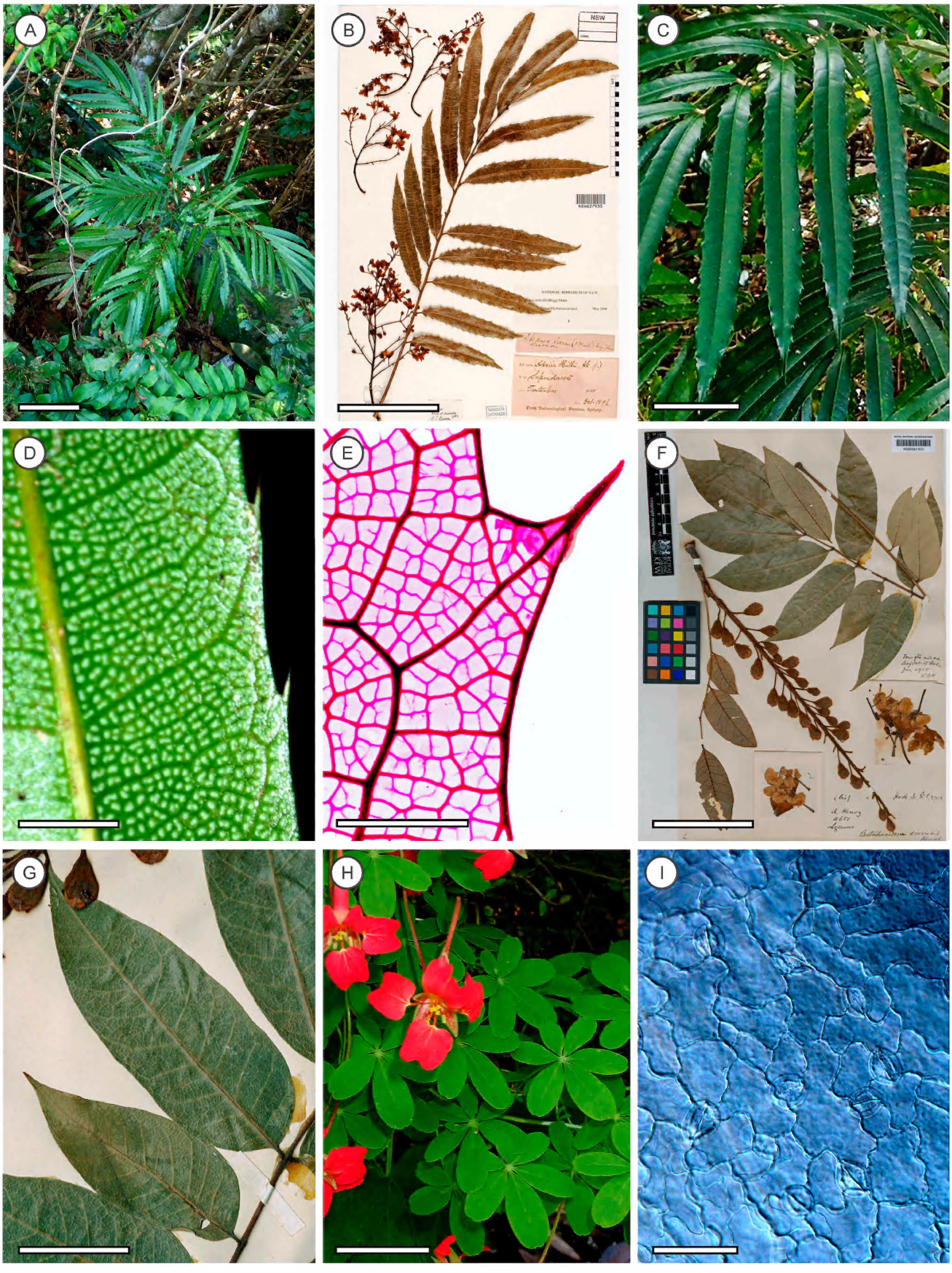
Results

Although leaves of *Akania* have not been recovered from Foulden Maar, the presence of fossil flowers there, fossil leaves and wood in South America and living plants in Australia suggests that they should be found in other Southern Hemisphere Cenozoic fossil deposits. Some of the distinguishing features of leaf teeth and venation that allowed placement of their fossils into *Akania* were illustrated by Romero & Hickey (1976) and discussed further by Gandolfo *et al.* (1988) and Iglesias *et al.* (2007). However, although Solereder (1899) gave a brief account of the leaf epidermis, there is currently no illustrated account of the venation and cuticles of the genus.

Leaves. Leaves up to 75 × 25 cm alternate, once-pinnate, petiolate, petiole to ~8 cm long, terete; leaflets 9–31, opposite, imparipinnate (Fig. 2A); blade attachment marginal; petiolules to 10 mm long, swollen-terete (Fig. 2B). Leaflets lanceolate to oblanceolate, 10–30 × 1–2 cm, coriaceous, toothed; apex bluntly acuminate; base cuneate, acute; adaxially more or less glabrous (Fig. 2C), abaxial surface areolate, white-dotted with clumps of papillae concealing stomata (Fig. 2D); margins pungent-toothed, one order of teeth, tooth spacing regular, ~1 cm^{-1}, sinus rounded, tooth shape CC/CC (concave/concave sensu Ellis *et al.* 2009); principal vein terminating at the tooth apex (Fig. 2E). Venation simple, pinnately brochidodromous, raised abaxially, forming a network of sunken areoles; secondary vein spacing regular, uniform, excurrent, interior secondary and intersecondary veins absent, marginal secondary veins present; tertiary and higher vein orders irregular reticulate; areolation prominent, free vein endings absent (Fig. 2E).

Cuticle. Adaxial cuticle thin, epidermal cells irregularly isodiametric, 16–44 µm wide (average 26 µm); outer surface of epidermal cells smooth, periclinal walls slightly raised (Figs 3A, 4A); inner surface anticlinal walls straight/curved to slightly undulate with relatively broad short flanges, appearing as slightly raised walls (Fig. 4B), inner periclinal walls granular (Fig. 4B),

Fig. 2. *Akania* (**A–E**), *Bretschneidera* (**F**, **G**) and *Tropaeolum* L. (**H**, **I**) habit and leaves. **A *Akania bidwillii*** habit, growing in rainforest at Hayters Hill Nature Reserve, N.S.W. (*JGC 3965*, NE); **B** Herbarium specimen showing 1-pinnate leaves and paniculate inflorescences (NSW627935); **C** Linear-lanceolate leaflets with prominent teeth (*JGC 3965*); **D** Portion of a leaf showing venation, areolate papilla clusters and distinctive marginal spines (*JGC 3965*); **E** Portion of a cleared leaf to show venation detail and characteristic marginal spine (NE20021). **F *Bretschneidera sinensis*** herbarium specimen showing 1-pinnate leaves and racemose inflorescences (K000681003);



G Broadly-lanceolate leaflets showing entire margins and slightly asymmetrical bases (K000681003). **H** ***Tropaeolum speciosum*** Poepp. & Endl., habit showing peltate leaflets, adventive in the Town Belt, Dunedin, New Zealand. **I** ***Tropaeolum majus*** L., abaxial cuticle with unornamented anomocytic stomata (*JGC 4006*). Herbarium specimens reproduced with permission: B The Royal Botanic Gardens & Domain Trust, http://plantnet.rbgsyd.nsw.gov.au/ (photo: B. Araghi, PlantNET); F, G Board of Trustees of the Royal Botanic Gardens, Kew, http://specimens.kew.org/herbarium/K000681003. Scale: A = 20 cm; B, E, F = 5 mm; C, H = 20 mm; D = 10 mm; G = 1 mm; I = 50 µm.

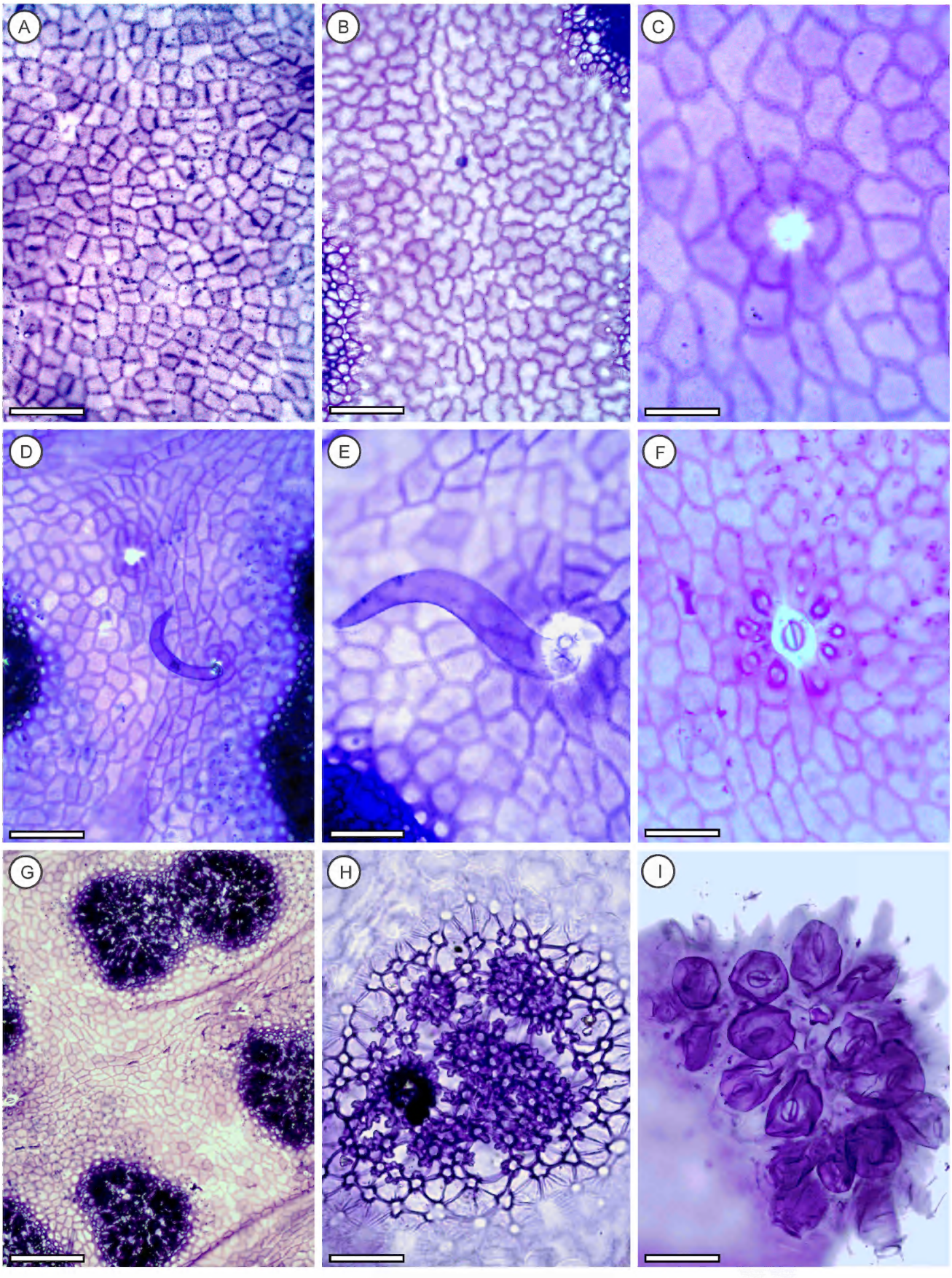


Fig. 3. Light microscopy of ***Akania bidwillii*** cuticles (NE20021). **A** Adaxial surface (appearing 'fuzzy' due to finely granular inner periclinal walls); **B** Abaxial surface away from papillate clusters; **C** Porate adaxial trichome base with surrounding cells; **D** Abaxial trichome and trichome base close to vein; **E** Detail of simple abaxial trichome; **F** Hydathode with papillate surrounding cells; **G** Arrangement of papillate (stomatal) clusters on abaxial surface; **H** Single enlarged cluster showing outer simple and inner coronulate papillae; **I** Detail of H. Scale: A, B, D = 100 µm; C, E, F, H = 50 µm; G = 200 µm; I = 20 µm.

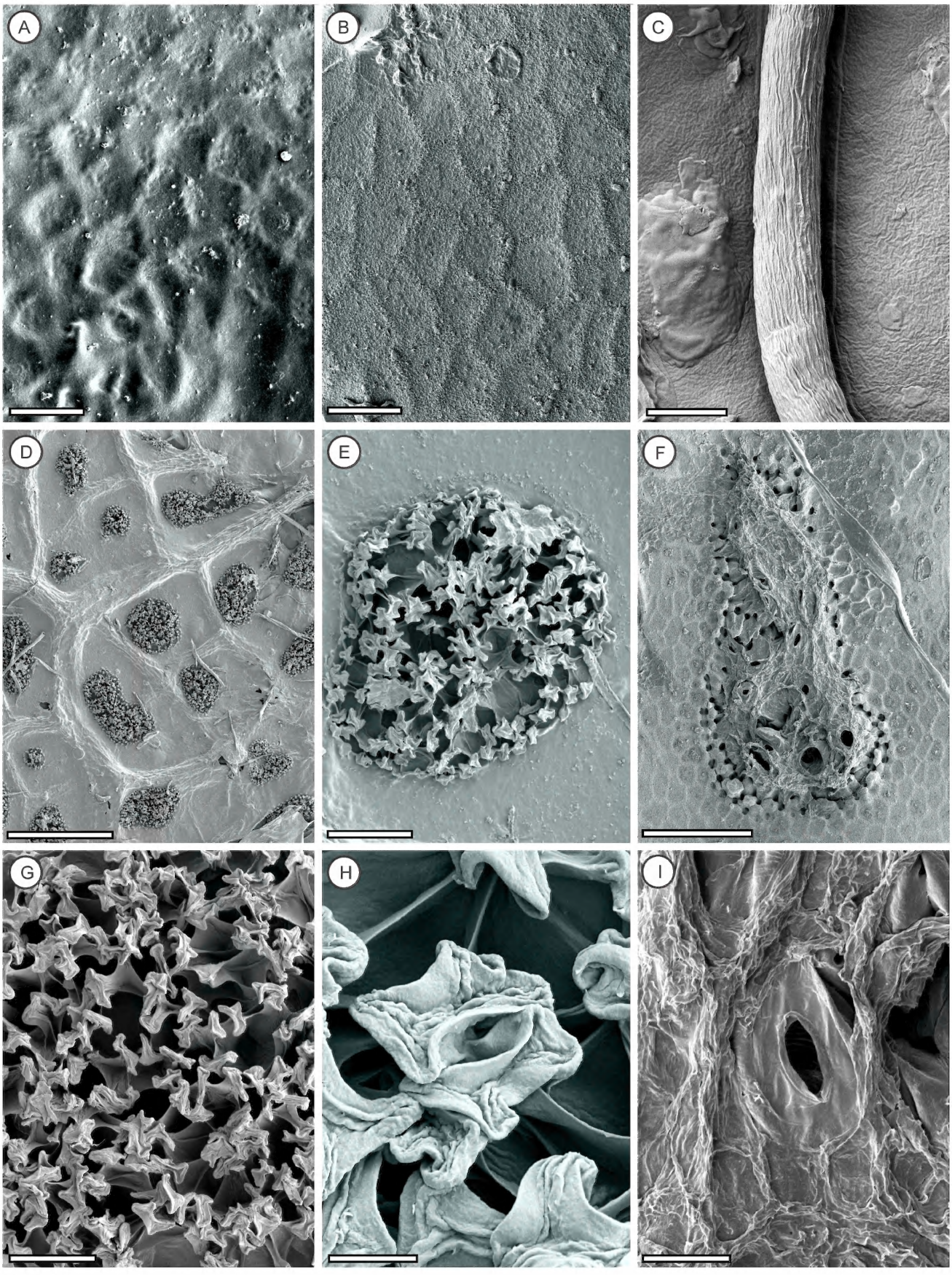


Fig. 4. SEM of ***Akania bidwillii*** leaves (NE20021). **A** Adaxial outer surface showing raised periclinal walls; **B** Adaxial inner surface showing short flanges (appearing as slightly raised walls) and fine periclinal granulation; **C** Detail of trichome with sculpturing of fine ridges; **D** Abaxial areolar surface to show stomatal groups; **E** Single cluster showing central coronulate papillae with simpler surrounding papillae; **F** Inner abaxial surface showing a few indistinct stomata and papilla bases; **G** Coronulate papillae; **H** Detail of lobed and striated papilla head with interconnecting ridges; **I** Inner surface of abaxial surface showing a single stoma. Scale: A–C = 25 µm; D = 500 µm; E, G = 50 µm; F = 100 µm; H = 10 µm; I = 20 µm.

making the cuticle appear 'fuzzy' under TLM (Fig. 3A). Trichomes short (<1 mm), simple, non-septate (Fig. 3C, E), thin walled with fine striations (Fig. 4C); trichome base slightly sunken in the epidermis, consisting of a pore and about six surrounding cells (Fig. 3C).

Abaxial cuticle thin, veins raised to form a network of sunken areoles; cuticle over the veins ridged, but smooth over the areolar surface (Figs 3D, E, 4D). Anticlinal epidermal cells irregularly isodiametric, 23–50 µm wide (average 35 µm), walls undulate, flanges short, wide and granular, appearing as slightly raised walls (Fig. 3B); periclinal walls granular. Trichomes few, similar to those present on the adaxial surface. One hydathode was seen with nine surrounding simple papillae (Fig. 3F).

Stomata in tight clusters surrounded by coronulate papillae, usually only 1–2 clusters per areole (Figs 3G, 4D); hidden by the papillae; anomocytic (Fig. 4F, I), small (10–14 µm, average 12 µm). Central papillae in the stomatal clusters coronulate, the large heads are irregularly lobed and striated (Figs 3H, I, 4E, G, H), the lower part of these papillae also striated; adjacent papillae connected by ridges (Fig. 4H). In some places coronulate heads coalesce to form a central cover with simpler papillae at the periphery (Figs 3H, 4E).

Discussion

Akania leaves resemble those of *Bretschneidera* in being alternate, imparipinnate and in having papillate cuticles (Bayer & Appel 2003a); however, *Bretschneidera* leaflets are broadly lanceolate with entire margins (Fig. 2F, G), whereas *Akania* leaflets are linear-lanceolate with prominent marginal teeth (Fig. 2B–E) and have papillae that form macroscopic clumps on the abaxial lamina (Fig. 2D; Solereder 1899). The leaves of *Tropaeolum* are also alternate, but vary from digitately pinnate to lobed, entire, or peltate (Fig. 2H) and unlike Akaniaceae, stipules are sometimes present (Bayer & Appel 2003b).

The cuticles of *Akania* are similar to those reported for *Bretschneidera* by Qiao *et al.* (2010) and Tu *et al.* (2012), particularly in the presence of distinctive, interconnected papillae surrounding the anomocytic stomata and the presence of simple unicellular trichomes and hydathodes derived from modified stomata. However, *Akania* bears macroscopic papilla clusters that cover the stomata (Figs 3G–I, 4E–H), whereas *Bretschneidera* has scattered stomata, each surrounded by microscopic papillae. Tropaeolaceae cuticles share anomocytic stomata (Fig. 2I), simple few-celled trichomes and vein-associated hydathodes with Akaniaceae, but lack the characteristic stomatal-associated papillae seen in the latter (Metcalfe & Chalk 1950; Weber & Kenda 1952; Bayer & Appel 2003a).

Despite more than 25 years of fossil collection at Foulden Maar by Pole (1993, 1996) and the current research team led by Assoc Prof. Daphne Lee at Otago University, including anatomical investigations of over 1000 mummified leaves (see summaries in Lee *et al.* 2012, 2016), no cuticle-bearing leaves or dispersed cuticle samples that match *Akania* have been reported to date, or any other fossil site in New Zealand, South America or Australia. This may be due to the leaves possessing very thin cuticles that are not easily preserved as fossils.

Leaflet impressions of extinct fossil *Akania* species (without cuticle) matching closely to those of the living species described here have been preserved at several sites in South America (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007). These Paleogene leaflet fossils were identified using a combination of the distinctive teeth, as well as shared characteristics of the secondary and higher-level venation, areolation, veinlet and intercostal areas. In particular, they share pinnately brochidodromous secondary venation, a fimbrial vein, keeled and ribbed midvein and spinose, irregularly spaced, CC/CC teeth (Gandolfo *et al.* 1988). These features were considered in combination to be characteristic of *Akania* leaflets by Romero & Hickey (1976), Gandolfo *et al.* (1988) and Iglesias *et al.* (2007). In contrast, although the basic venation pattern in *Bretschneidera* is also pinnately brochidodromous with similar higher vein order orientation to *Akania*, it has broader, asymmetrical and entire-margined leaflets and lacks all of the tooth-related characteristics of the latter (Fig. 2F, G).

Fossil Akaniaceae pollen is only known from the flowers found at the Miocene-aged Foulden Maar site in New Zealand, possibly because the thin walls of the fossil pollen makes fossilisation less likely (Conran *et al.* 2019). As summarised in Conran *et al.* (2019), the pollen of the fossil has a more well-defined reticulum, especially in polar areas, the colpi are short and narrow, with indistinct margins. The exine and sexine of the fossil is thinner than in the living *A. bidwillii* and has a much finer reticulum with more evenly sized luminae than *Bretschneidera* and lacks luminal granulae. Nevertheless, both living genera share medium sized tricolpate pollen with short colpi and a well-defined reticulum with variable-sized luminae. In contrast, Tropaeolaceae pollen is tricolporate with a reticulate to partially striate exine and granulate luminae (Erdtman 1986; Bayer & Appel 2003b), agreeing with the placement of these families in the lower Brassicales. The fossil *Akania* pollen does somewhat resemble the palynomorph *Tricolpites densipunctatus* D.J.McIntyre of unknown affinity from the early Miocene of New Zealand (McIntyre 1968; Raine *et al.* 2011). However, although the pollen of the latter is tricolpate with a microreticulate and punctate exine, its grains are approximately half the size and the colpi are long and narrow with straight, well-defined margins.

Akaniaceae are thought to have diverged from Tropaeolaceae in the Late Cretaceous (Cardinal-McTeague *et al.* 2016), with subsequent dispersal to Australia and New Zealand and then on to China

(Wang *et al.* 2018) and India (Kumar *et al.* 2017). The differentiation of the two living genera and the fossil history and biogeography of Akaniaceae was summarized by Conran *et al.* (2019), where the reasons for the family's disjunct distribution were explored. Based on molecular studies of the lower Brassicales (Cardinal-McTeague *et al.* 2016) and the presence in South America of leaf impressions possessing the characteristic marginal teeth of *Akania* (Fig. 2F) going back to the Palaeocene (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007), a South American origin for the family is suggested. The discovery of Miocene-aged fossil *Akanioxylon* Brea, Zucol, Bargo, Fernicola & Vizcaíno wood (Brea *et al.* 2017) in Argentina further supports this, with Carlquist (1996) and Brea *et al.* (2017) both noting that the wood anatomy of *Akania* and *Bretschneidera* is almost identical. The apparent wide Southern Hemisphere distribution of the family throughout the Cenozoic and its subsequent expansion into Asia means that further fossils displaying the distinctive leaves and cuticles of Akaniaceae could well be collected South America, Australasia, China and possibly India.

However, because this South American origin hypothesis is conditional on older, unequivocal Akaniaceae fossils not being found elsewhere, the ability to identify fossilised leaves of *Akania* and *Bretschneidera* is critical for evolutionary and biogeographic studies of the lower Brassicales. The present study suggests that in addition to a woody habit and large, pinnately-compound leaves, the presence of interconnected coronulate abaxial papillae on the leaves are a synapomorphy for Akaniaceae, distinguishing them anatomically from their herbaceous sister family Tropaeolaceae, which has unornamented abaxial cuticles. Within Akaniaceae, the two living *Akania* and *Bretschneidera* species can also be distinguished easily, both by the lack of teeth on the leaflets of the latter, but more importantly (as leaflet toothing may be different in extinct taxa) by the scattered papillae of *Bretschneidera* in contrast to the tightly clustered and stomate-associated papilla clumps in *Akania*. Because both the family and the two extant genera can be recognised readily from leaf cuticles, this will assist in the definitive identification of any new Akaniaceae macrofossils or dispersed cuticle samples.

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SHORT COMMUNICATION

Validation of four new combinations in *Eucalyptus* (Myrtaceae) from south-western Western Australia

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Four new combinations were proposed in French & Nicolle (2019) for *Eucalyptus* taxa from the south-west region of Western Australia, but these did not meet the requirements for valid publication under Article 41.5 of the *International Code of Nomenclature for algae, fungi, and plants* (Turland *et al.* 2018), because a full and direct reference to the place of publication for each intended basionym was not provided. In the book, for each new combination, the intended basionym and a bibliographic citation of the work in which it was published was given, but the *References* list provided only the pagination of that whole publication, not the specific page on which the basionym was published. These new combinations, based on names published by Brooker (1986) and Brooker & Hopper (1991), are validated here.

Eucalyptus improcera (Brooker & Hopper) D.Nicolle & M.E.French, *comb. et stat. nov.*

Eucalyptus densa subsp. *improcera* Brooker & Hopper, *Nuytsia* 8(1): 154 (1991). — **Holotype:** 7.2 km W along Aerodrome Road from Lake King–Ravensthorpe road [Newdegate–Ravensthorpe Road], Western Australia, 19 May 1987, *M.I.H.Brooker 9646 & P.Grayling* (PERTH). **Isotypes:** AD, CANB, MEL, NSW.

Eucalyptus improcera D.Nicolle & M.E.French, *Eucalypts W. Austral. S.W. Coast & Ranges* 140, *nom. inval.*

Detailed description, notes and illustrations for this species are provided in French & Nicolle (2019: 140–141).

Eucalyptus redunca subsp. *pluricaulis* (Brooker & Hopper) D.Nicolle & M.E.French, *comb. et stat. nov.*

Eucalyptus pluricaulis Brooker & Hopper, *Nuytsia* 8(1): 155 (1991). — **Holotype:** Depression W of intersection of Mudge Rd and Coorow–Greenhead Road, Western Australia, 21 May 1982, *M.I.H.Brooker 7522* (CANB). **Isotypes:** CANB, NSW.

Eucalyptus redunca subsp. *pluricaulis* M.E.French & D.Nicolle, *Eucalypts W. Austral. S.W. Coast & Ranges* 146 , *nom. inval.*

Detailed description, notes and illustrations for this subspecies are provided in French & Nicolle (2019: 146–147).

Eucalyptus redunca subsp. *porphyrea* (Brooker & Hopper) D.Nicolle & M.E.French, *comb. nov.*

Eucalyptus pluricaulis subsp. *porphyrea* Brooker & Hopper, *Nuytsia* 8(1): 161 (1991). — **Holotype:** 57.8 km south of Jerramungup on Albany road [South Coast Highway], Western Australia, 10 Apr. 1983, *M.I.H.Brooker 8082* (PERTH). **Isotypes:** CANB, NSW.

Eucalyptus redunca subsp. *porphyrea* M.E.French & D.Nicolle, *Eucalypts W. Austral. S.W. Coast & Ranges* 144, *nom. inval.*

Detailed description, notes and illustrations for this subspecies are provided in French & Nicolle (2019: 144–145).

Eucalyptus redunca Schauer subsp. *redunca*

The present publication also establishes the autonym *Eucalyptus redunca* Schauer subsp. *redunca*. Detailed description, notes and illustrations for this subspecies are provided in French & Nicolle (2019: 142–143).

Eucalyptus virella (Brooker) D.Nicolle & M.E.French, *comb. et stat. nov.*

Eucalyptus celastroides subsp. *virella* Brooker, *Nuytsia* 5(3): 359 (1986). — **Holotype:** 13.2 km north-east of Calingiri on Wongan Hills road, Western Australia, 28 Aug. 1983, *M.I.H.Brooker 8283* (holo: PERTH). **Isotypes:** AD, BRI, CANB, K, MEL, NSW.

Eucalyptus virella D.Nicolle & M.E.French, *Eucalypts W. Austral. S.W. Coast & Ranges* 224, *nom. inval.*

Detailed description, notes and illustrations for this species are provided in French & Nicolle (2019: 224–225).

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Grammosolen (Solanaceae - Anthocercideae) revisited

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Abstract: Study of newly collected specimens from beyond the former known geographical range of *Grammosolen*, together with consideration of newly published results of molecular phylogenetic studies in tribe Anthocercideae have led to an expanded concept of the genus. The rare *G. archeri* Haegi is newly described from far south-eastern Western Australia; *G. odgersii* is transferred from *Cyphanthera*; and the known range of *G. truncatus*, formerly regarded as an endemic South Australian species, is extended to adjacent far eastern Western Australia.

Keywords: *Grammosolen*, *Cyphanthera*, Anthocercideae, Solanaceae, taxonomy, new species, intergeneric hybrids

Introduction

Grammosolen Haegi was first described as a new genus in the context of a monographic study leading to the re-instatement of the distinctively Australasian tribe Anthocercideae G.Don (Haegi 1981, 1983). The study led to the recognition of 31 species in seven genera–*Anthocercis* Labill., *Anthotroche* Endl., *Crenidium* Haegi, *Cyphanthera* Miers, *Duboisia* R.Br., *Grammosolen* and *Symonanthus* Haegi (Haegi 1981, 1983). *Grammosolen* was established to accommodate two closely related, distinctive species: *G. dixonii* (F.Muell. & R.Tate) Haegi (formerly mistakenly assigned to *Newcastelia* F.Muell. in family Verbenaceae) and *G. truncatus* (Ising) Haegi, originally described as a species of *Anthotroche*. One new species has since been described in each of *Anthocercis* (Macfarlane & Wardell-Johnson 1996) and *Duboisia* (Craven *et al.* 1995), bringing the total to 33 species in the tribe.

Grammosolen has been known only from the state of South Australia. Additional collecting in more remote parts of Australia has since not only extended the known distribution in South Australia but has also brought to light specimens from Western Australia. Some of these represent a range extension of *G. truncatus* a relatively short distance across the border from South Australian populations nearby. Others, confined to a small area much further west, inland from Cape Arid on the southern coast, have proved to be not readily assignable to either existing species, or to any other species in the tribe. These specimens are consistently distinct in several features, including their small, orbicular-reniform to obcordate leaves and in their smaller flowers and fruits. The new species *Grammosolen archeri*, endemic to south-eastern Western Australia, is described here on the basis of these specimens.

Materials and Methods

This study is based on investigations carried out over several decades, commencing in the first instance as part of the subject of a PhD thesis (Haegi 1983). It is based on detailed morphological examination of all available herbarium material in Australian and relevant overseas herbaria as well as many specimens collected in the course of the study. Measurements of each character used in the descriptions were, where possible, taken from a sample of between 20 and 30 specimens selected to represent the whole geographic range. Characters which showed variability were measured for at least two organs on each specimen in the sample and in the case of leaves, the dimensions of the largest as well as of two or three of those judged to be close to the mode were recorded. Dried material was used for all measurements, except the flowers which were either softened in a weak solution of detergent and hot water or for which spirit material collected in the course of the study was used. Leaves were measured to the nearest millimetre with a ruler, while most other organs were measured to the nearest ½ millimetre using a low-power stereo-microscope fitted with an ocular micrometer, at 10× magnification. Larger hairs (1.0–2.5 mm long) were measured in this way to the nearest 0.05 mm; smaller hairs (0.025–0.075 mm) were measured to the nearest 0.025 mm at 40× magnification. Indumentum terminology follows Haegi (1991).

Chromosome numbers were investigated for three species from the study of meiosis in pollen mother cells. To date it has not been possible to obtain living material of the fourth species, *G. archeri*. Flower buds collected in the field were placed immediately in a mixture of 3 parts of ethanol to 1 part of glacial acetic acid (mixed in situ). After 24 hours the buds were transferred to 100% ethanol, kept in cool conditions and finally

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stored in temperatures below 0°C. Standard anther squash techniques (Darlington & La Cour 1970) were used to obtain microscope slide preparations for observing chromosomes at meiosis. The preparation was examined with a compound light microscope at up to 1,000× magnification, sometimes with the aid of phase contrast illumination. The results were recorded using a camera lucida device fitted to the microscope.

Although it can be caused by other factors (such as environmental ones) sterility of pollen is a useful guide to the occurrence of hybridisation, especially when pollen from possible parents sampled at the same time proves highly viable. Stainability of pollen was tested as an indicator of viability using 0.5% lactophenol cotton blue, which stains cytoplasm. Pollen from a single mature anther from each of several different flowers from recently collected herbarium specimens was teased out into a drop of stain on a microscope slide, a coverslip was applied and the preparation examined with a compound microscope, with all grains present scored.

The composite distribution map (Fig. 3) was prepared utilising point distributional data from the AVH, viewed in the ALA portal (accessed 3 July 2019), downloaded and edited to remove misidentified and misplotted duplicate records. The map as presented was prepared using QGIS v. 3.2.0–Bonn, with the map outline and features (coastline, sand-ridge and lakes layers) from GEODATA TOPO 250K series 3 Topographic data (Geoscience Australia 2018, accessed 5 February 2018).

Generic placement of *Cyphanthera odgersii*

When it was described, *Grammosolen* was unique within the Anthocercideae for the occurrence of multangulate hairs (in particular on the exterior of the corolla lobes), a di- or tri-dynamous androecium of five fertile stamens and a gametic chromosome number of n=56. At that time attention was drawn to some close similarities between *Cyphanthera odgersii* (F.Muell.) Haegi and the two known species of *Grammosolen*. Verticillately-branched trichomes are found in both *C. odgersii* and *G. dixonii*, while all three species share a spike-like inflorescence and, perhaps most notably, hippocrepiform anthers (Haegi 1983). These last two features are not otherwise found in *Cyphanthera* (Haegi 1983). However, like all species of *Cyphanthera* for which a count had been determined (*C. albicans* (A.Cunn.) Miers, *C. microphylla* Miers, *C. myosotidea* (F.Muell.) Haegi and *C. tasmanica* Miers), *C. odgersii* has a gametic chromosome number of n=30 (Haegi 1983). On balance, *C. odgersii* was included within *Cyphanthera* rather than in *Grammosolen* for that reason and because it shared with all the other species a corolla glabrous outside and a didynamous androecium of only four stamens. This classification has been widely adopted since that time.

More recently, molecular phylogenetic studies of the Anthocercideae and near relatives, analysing sequence data from four chloroplast DNA regions — *ndh*F and *trn*L/F (Garcia & Olmstead 2003), as well as *trn*S-G and *mat*K (Clarkson *et al.* 2004) — have provided new evidence for assessing the affinities and relationships of these genera. It is now generally accepted that together with the genus *Nicotiana*, these genera make up a distinctive grouping within the family, for the time being treated as subfamily Nicotianoideae. This is confirmed and placed within the context of an overview of the molecular phylogeny of the Solanaceae as a whole by Olmstead *et al.* (2008). There is strong support for continued recognition of Tribe Anthocercideae (Clarkson *et al.* 2004), perhaps with some uncertainty about the placement of the genus *Symonanthus*, whose relationships with the remainder of the Anthocercideae on the one hand and *Nicotiana* on the other, remain unresolved (Olmstead *et al.* 2008). Within the Anthocercideae these molecular phylogenetic studies provide partial support for the morphologically-based generic classification (including continued generic recognition of *Grammosolen*) but also provide evidence for a different approach to the circumscription of some genera. On the basis of that evidence *C. odgersii* is demonstrated, as part of a highly supported "*Grammosolen* clade", to have a closer relationship with the two known species of *Grammosolen* than to all the other species of *Cyphanthera* (Garcia & Olmstead 2003; Clarkson *et al.* 2004).

The evidence from molecular studies prompts a re-assessment of the diagnostic value of characters found in *Grammosolen* and *Duboisia*/*Cyphanthera*. Inclusion of *Cyphanthera odgersii* in the *Grammosolen* clade on molecular grounds is consistent with the shared occurrence of erect, hippocrepiform anthers dehiscing by a hippocrepiform slit on the abaxial face (Figs 1, 10, 11). This may prove to be a synapomorphy for the expanded genus (together with the otherwise distinctive genus *Anthotroche*). In the apparent plesiomorphic condition found throughout *Duboisia* (four species) and the remainder of *Cyphanthera* (eight species) the anthers are sub-reniform, oblique (twisted towards the vertical and tilted abaxially) and dehisce by a semicircular slit along the distal margin (for example as in *C. racemosa* (F.Muell.) Haegi – Fig. 1). While a dense indumentum of dendritic hairs occurs in some species of *Cyphanthera*, the very dense woolly indumentum found in *C. odgersii* is unique in the genus (Haegi 1991). Similar hair-coverings are, however, found in *Grammosolen* and *C. odgersii* shares elaborate verticillately branched hairs with *G. dixonii*. Similarly the spike-like inflorescence of *C. odgersii* is unique in *Cyphanthera* but occurs in all species of *Grammosolen*, being particularly well developed in *G. dixonii*. Flowers with only four fertile didynamous stamens are characteristic of all *Cyphanthera* species. In *Grammosolen* the androecium consists of five fertile, di- or tri-dynamous stamens; this is probably the plesiomorphic condition. If *C. odgersii* is correctly placed in *Grammosolen*, it is possible that the loss of the fifth fertile stamen arose independently

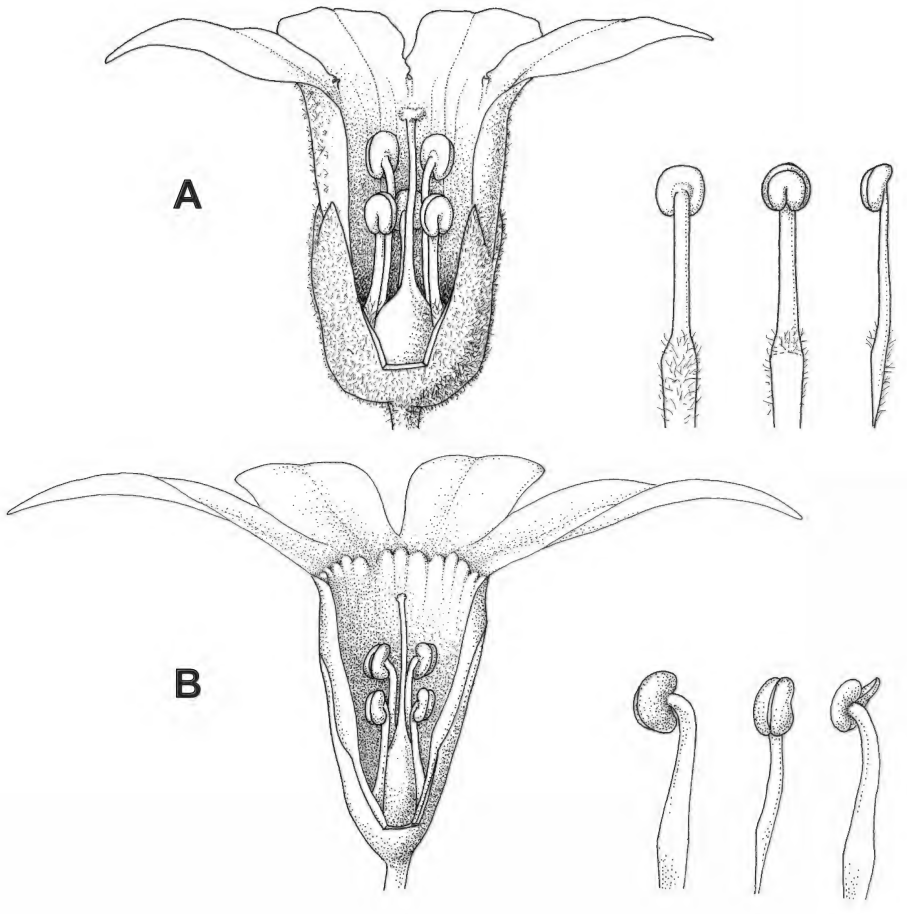

Fig. 1. Semi-schematic representation of anther types in *Grammosolen* and *Cyphanthera*, showing flowers with part of calyx and corolla removed to reveal stamens, together with excised stamens depicting dorsal (abaxial), ventral (adaxial) and lateral views of anthers. **A** *Grammosolen* (*G. dixonii – Haegi 868G*, × 8.5); **B** *Cyphanthera* (*C. racemosa* (F. Muell.) Haegi – *Haegi 1957* (NSW, CBG, PERTH), × 7). Illustration by R. Roden.

in this species, separately from the event which resulted in this condition in *Cyphanthera* and *Duboisia*. Alternatively, the presence of a fifth fertile stamen in the other three species of *Grammosolen* could represent a reversion. The ontogenetic likelihood of such a reversion would require further investigation. Some insight may be evident in the variable occurrence of flowers with four or five fertile stamens in the related species *Crenidium spinescens* Haegi: the absence of one of the fertile stamens could be the result of genetic masking rather than its irreversible loss.

The multangulate hairs found in all species of *Grammosolen*, but absent throughout *Cyphanthera*, may have been secondarily lost in *C. odgersii* as a member of the *Grammosolen* clade or may have evolved subsequently in the other species. Chromosome numbers in the tribe were first counted by Barnard (1949) who recorded n=30 and 2n=60 for *Duboisia leichhardtii* and *D. myoporoides*. Ikanaga *et al.* (1979) added a count of n=?28 for *D. leichhardtii* and confirmed n=30 for *D. myoporoides*. Further investigations by Haegi (1981, 1983), resulted in the first chromosome number determinations for *Symonanthus*, *Anthocercis*, *Cyphanthera*, *Grammosolen*, *Anthotroche* and *Crenidium*. To the extent that counts were obtained (for 21 of the 31 species), a strong correlation was demonstrated with morphological features characterising genera (Haegi 1981, 1983). A gametic chromosome number of n=30 was observed for five of the nine species of *Cyphanthera* (including *C. odgersii*) while the only two species of *Grammosolen* known at the time produced counts of n=56 (Haegi 1983). Given it seems likely that n=56 represents the derived state, the occurrence of the plesiomorphic state in the clade (n=30 in *C. odgersii*) is not problematic.

On the basis of the compelling evidence from the molecular phylogenetic studies and the assessment above, *C. odgersii* is here transferred to *Grammosolen*, with the generic circumscription emended accordingly. This transfer creates no nomenclatural problems at any level. The species epithet has not been used previously in *Cyphanthera* and the lectotype species of the genus designated by Hunziker (2001) is *C. ovaliflolia* Miers (currently regarded as a taxonomic synonym of *C. albicans* (Cunn.) Miers subsp. *albicans*; Purdie *et al.* 1982; Haegi 1983).

Occurrence of putative intergeneric hybrids in the Anthocercideae

The possible occurrence of several intergeneric hybrids was recorded by Haegi (1983) and investigations of the alkaloid chemistry of some of these putative hybrids, together with the putative parents (El Imam *et al.* 1991) provided supporting evidence. Two of the recorded hybrids involve *Grammosolen*, with one species, *G. dixonii*, being one of the putative parents in each instance. This is reported on in more detail under *G. dixonii* below.

Taxonomy

Grammosolen Haegi

Telopea 2 (1981) 178. — **Type species:** *Grammosolen dixonii* (F. Muell. & R.Tate) Haegi

Newcastelia auct. non F.Muell.: F.Muell. & Tate, *Trans. & Proc. Roy. Soc. S. Austral.* 10 (1888) 81, p.p. as to *N. dixonii* (= *Grammosolen dixonii*); J.M.Black, *Fl. S. Austral.* 3 (1926) 479, p.p. as to *N. dixonii*, excl. W.A. material; C.A.Gardner, *Enum. Pl. Austral. Occ.* 3 (1931) 111, p.p. as to *N. dixonii*, excl. W.A. material; J.M.Black, *Fl. S. Austral.* edn. 2, 4 (1957) 721, p.p. as to *N. dixonii*, excl. W.A. material; Beard, *Descr. Cat. W. Austral. Pl.* (1965) 92, p.p. as to *N. dixonii*, wrongly recorded for W.A.

Anthotroche auct. non Endl.: Ising, *Trans. & Proc. Roy. Soc. S. Austral.* 46 (1922) 605, t. 38, 39, Fig. 1, p.p. as to *A. truncata* (= *Grammosolen truncatus*); J.M.Black, *Fl. S. Austral.* 3 (1926) 500, p.p. as to *A. truncata*; *Fl. S. Austral.* edn 2, 4 (1957) 754, p.p. as to *A. truncata*; N.T.Burb., *Dict. Austral. Pl. Gen.* (1963) 20, p.p.; H.Eichler, *Suppl. J.M. Black's Fl. S. Austral.* (1965) 226, 273, p.p. as to *Newcastelia dixonii* and *Anthotroche blackii* as applied to S.A. specimens including all those cited; D'Arcy in Hawkes, R.N.Lester & A.D.Skelding, *Biol. Taxon. Solanac.* (1979) 12, 14, 17, 21, p.p.; Haegi, ibid, 121–124, p.p.

Anthocercis auct. non Endl.: F.Muell., *Fragm.* 10 (1876) 19, p.p. as to *A. odgersii* (= *Grammosolen odgersii*, q.v.).

Cyphanthera auct. non Miers: Haegi, *Telopea* 2(2) (1981) 177; R.W.Purdie, Symon & Haegi, *Fl. Austral.* (1982) 27; Hunziker, *Gen. Solanac.* (2001) 386–388, all p.p. as to *C. odgersii* (= *Grammosolen odgersii*).

Erect ± leafy, taprooted *shrubs*, suckering from stem base following damage to or removal of aerial parts, densely tomentose with variously dendritic hairs on all vegetative parts, with corky fissured bark at stem base. *Leaves* alternate, petiolate to subsessile, entire. *Flowers* bisexual, protogynous, subtended by a pair of opposite or sub-opposite bracts, borne in leafy clusters of cymes terminating condensed lateral branchlets, shortly pedicellate. *Calyx* ± cyathiform, 5-lobed, persistent, lanate-tomentose. *Corolla* ± narrowly tubular with ± regular (4–) 5 (–6)-lobed patent limb, drab white with violet striations in throat [but unknown in *G. archeri*], glabrous or glandular-hairy outside, glabrous inside except for the very densely and minutely papillose lobes; *aestivation* of lobes ± induplicate, the margins of each lobe overlapping each other or ± meeting, the lobes free and erect; *tube* ± narrowly funnel-shaped; *lobes* broadly ovate to narrowly elliptic with truncate base, very densely and minutely papillose on upper (inner) surface, otherwise glabrous. *Stamens* epipetalous at base of corolla-tube, 4 or 5, usually didynamous, very rarely tridynamous, slightly recurved prior to and ± erect at anthesis, included in the corolla-tube; *anthers* much shorter than filaments, unilocular, free, erect, hippocrepiform, dehiscing by an abaxial hippocrepiform slit. *Ovary* 2-locular, surrounded at base by a moist, annular, aromatic but non-nectariferous disc; *ovules* few; *style* included; *stigma* ± capitate, very shortly bilobed. *Fruit* a smooth capsule with marginicidal and loculicidal, septifragal dehiscence into 4 valves, somewhat concealed by the dense, long indumentum of subtending branchlet and calyx; *calyx* non-accrescent but as long as or longer than capsule; *seeds* few, subreniform with reticulate testa; *embryo* slightly curved, not coiled. *Gametic chromosome number* (determined for three of the four species) 30 or 56.

Distribution. As newly circumscribed, *Grammosolen* is a genus of four species; these have non-overlapping ranges, extending from the Avon Wheatbelt through the Coolgardie, Great Victoria Desert and Mallee regions in southern Western Australia, to the Great Victoria Desert, western Gawler Ranges, Eyre Yorke Block and the Murraylands in South Australia. All of the species occur as scattered, small populations on local patches of sandy

Key to species

1. Leaves 2.5–7 mm long, orbicular-reniform to obcordate (sometimes broadly ovate at shoot tips), L:B mostly 0.65–0.96; calyx 2.0–2.5 mm long . . . . . **3. *G. archeri***

1: Leaves 7–30 mm long, ovate, ovate-elliptic, ovate-triangular (sometimes broadly so) or subcordate, L:B mostly 0.8–3.8; calyx 2.5–7 mm long

2. Leaves conspicuously petiolate, with petiole 2–4 mm long; leaf base cuneate; indumentum very densely and closely tomentose with multangulate-dendritic hairs 0.05–0.15 mm long above and below . . . . . **2. *G. truncatus***

2: Leaves of subsessile appearance, with petiole 0.5–1.5 mm long, rarely 3 mm long in larger leaves; leaf base rounded-truncate, cordate, cuneate or attenuate; indumentum densely to very densely tomentose to lanate-tomentose with multangulate-dendritic and verticillately-branched hairs 0.2–1.0 mm long

3. Leaves ovate-triangular to very broadly so, sometimes subcordate; base rounded truncate, sometimes cordate or broadly cuneate; multangulate-dendritic and verticillately-branched hairs both present; leaves appressed or distally inclined, more or less overlapping; corolla lobes mostly 3–6 mm long; stamens 5 . . . . . **1. *G. dixonii***

3: Leaves broadly to narrowly elliptic, base cuneate to attenuate; indumentum consisting entirely of verticillately branched hairs (other than small, inconspicuous glandular hairs); leaves spreading; corolla lobes 1.3–2.5 mm long; stamens 4 . . . . . **4. *G. odgersii***

soil or in extensive dune systems, generally on disturbed sites within or in association with mallee vegetation.

1. *Grammosolen dixonii* (F.Muell. & R.Tate) Haegi

Telopea 2 (1981) 178; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 29; Haegi in Jessop & Toelken, *Fl. S. Austral.* edn 4, 3 (1986) 1242. — *Newcastelia dixonii* F.Muell. & Tate, *Trans. & Proc. Roy. Soc. S. Austral.* 10 (1888) 81, as '*Newcastlia Dixoni*'. — **Type citation:** "On sand ridges at Ral-Ral on the River Murray, 30 miles [c. 48 km] from the Victorian border; also at Crystal Brook; Mr Samuel Dixon." **Lectotype (here designated):** Ral Ral, S.A., *S. Dixon s.n.* (MEL41019). **Isolectotypes:** AD97221081A, BM629250. **Remaining syntype:** Crystal Brook, S.A., *S. Dixon s.n.* (AD97221081B).

Anthotroche blackii auct. non F.Muell.: H.Eichler, *Suppl. J.M. Black's Fl. S. Austral.* (1965) 273, p.p. as to all S.A. specimens cited.

Erect, spreading or sprawling greyish *shrub* 0.3–2 m tall and 0.8–3 (–5) m diam., with branches (at least finally) ascending. *Branches* very densely lanate-tomentose with multangulate-dendritic and verticillately branched hairs mostly 0.6–1.3 mm and fewer hairs c. 1.5 times as long as these i.e. 0.8–1.5 mm, and scattered, inconspicuous glandular hairs 0.1–0.4 mm, the indumentum gradually wearing off with age. *Leaves* loosely appressed or at least distally inclined, more or less overlapping so as to obscure much of the axis, subsessile or with a petiole to 1.5 (–3) × 1 mm; *lamina* ovate-triangular to very broadly so, sometimes subcordate (L:B (0.8–) 0.9–1.5 (–2.5)), (6–) 8–16 (–20) × (4–) 6–15 (–17) mm, densely to very densely tomentose (including petiole) with stalked multangulate-dendritic and verticillately branched hairs, mainly 0.1–0.3 mm and fewer 0.2–0.5 mm, and scattered inconspicuous glandular hairs, 0.05–0.1 mm, the branched hairs usually denser and up to 0.5 (–0.7) mm on the underside; *base* rounded-truncate, sometimes cordate or broadly cuneate; *apex* acute or slightly obtuse, less commonly acuminate, usually angular or blunt, rarely rounded; *margin* flat or often undulate, sometimes slightly recurved; midrib obscure adaxially, slightly prominent abaxially. *Flowers* borne in leafy clusters consisting of one to three, 1–3-flowered cymes on much-condensed lateral branchlets, sometimes aggregated to form leafy spikes; *inflorescence-bracts* 1–4 × 0.5–2 mm, moderately tomentose with multangulate-dendritic hairs. *Pedicel* 0.2–0.8 mm, oblique, glabrous. *Calyx* 3.3–5 mm, outside densely to very densely tomentose with eglandular multangulate-dendritic and verticillately branched hairs 0.2–0.3 (–0.8) mm and upper layer 0.4–0.8 (–2.0) mm, inside moderately pubescent with porrect to antrorse glandular hairs 0.05–0.15 mm, and multangulate-dendritic, forked or simple eglandular hairs 0.15–0.3 mm on the lobes, often only near the apex; *calyx-lobes* acute to slightly obtuse or rarely acuminate, always angular, (0.4–) 0.5–1.1 (–1.5) times as long as tube, 1.0–2.5 (–3) × 1–1.5 mm, sinuses acute. *Corolla* (7.5–) 8–12.5 mm, dull white with violet striations, outside moderately pubescent with multangulate-dendritic hairs 0.2–0.3 (–0.4) mm on the lobes and upper tube, inside very densely papillose with hairs 0.05–0.1 mm on lobes; *tube* 4.5–7.5 mm long., diam. 1.0–1.7 mm at base, 2.5–3.5 mm at limb-base; *lobes* ovate to elliptic with truncate base, (L:B 1.4–2.2 (–2.8)), 3–6 (–7.5) × (1.6–) 2–4 mm, slightly narrowed or broadened at the base, apex acute and usually blunt or rounded, rarely angular, margin flat. *Stamens* 5, the longer ones (3.5–) 4–5 mm and the shorter ones 2.5–3.5 (–4.2) mm; *filament-bases* and adjacent corolla moderately to densely pubescent with simple or forked eglandular hairs 0.2–0.5 (–0.8) mm, less dense abaxially; *anthers* 0.8–1.0 × 0.8–1.0 mm. *Ovary* very broadly ovoid to globose or depressed globose,

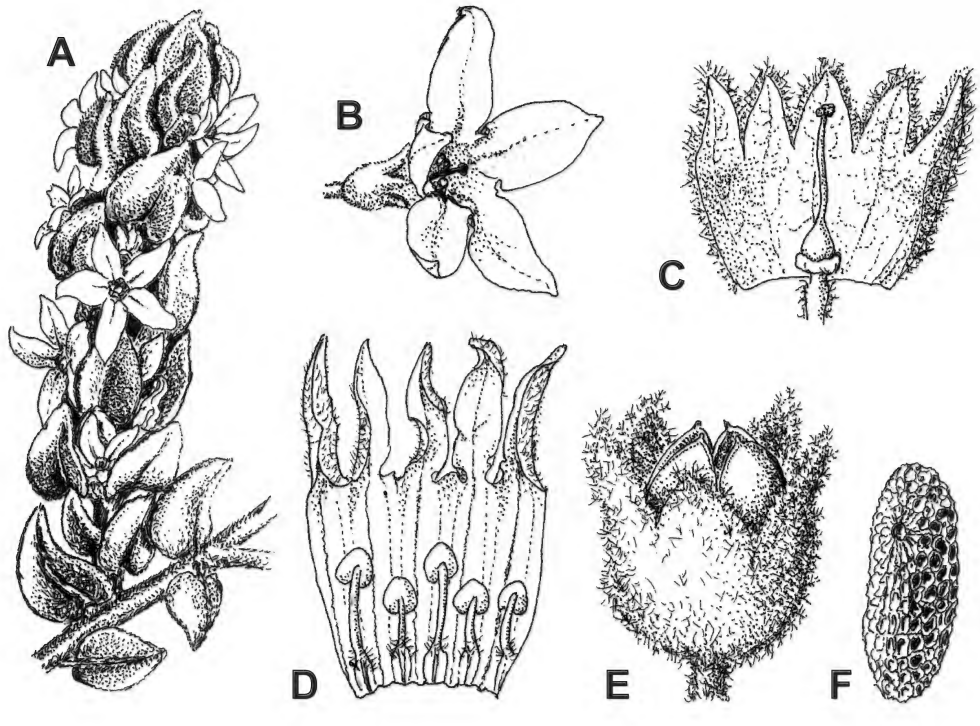

Fig. 2. *Grammosolen dixonii*. **A** flowering branchlet, × 1; **B** flower, × 2.5; **C** calyx of advanced bud opened out, with pistil, × 6; **D** opened corolla of same, × 6; **E** capsule, × 6; **F** seed, × 10. (A–D *Haegi 1331*; E–F *Haegi 869*). Illustration by M. Perkins.

0.6–1.2 × 0.6–1.2 mm; *ovules* 4–9 in total; *style* 2.7–3.5 (–4.2) mm, ± equal to the longer stamens and included by 0.5–2 mm; *stigma* c. 0.2 × 0.4 mm; *disc* undulate, 0.2–0.5 mm high, usually slightly, rarely much greater in diameter than the ovary (to 1.6 mm), red. *Capsule* ± inconspicuous, ± embedded in dense long hairs of enclosing calyx and axis, ± globose, 3.5–4.5 × 3–4.8 mm. *Seeds* 1–5, 2.5–3.5 × 1.1–1.6 mm; *surface-reticulae* 0.1–0.35 × 0.1–0.2 mm. *Chromosome number:* n=56 (*L. Haegi 676, 1457M*). **Fig. 2.**

Typification. This species was described (under the basionym, *Newcastelia dixonii*) by two authors, F. Mueller and R. Tate, and two localities are given in the protologue. Material corresponding with information in the protologue has been located on three sheets, one each in AD, BM and MEL. But for one piece on the AD sheet, these specimens all match one another and resemble material from the stated area of collection, viz. Ral-Ral on the River Murray. Although not labelled as such, the distinctive piece on the AD sheet, as indicated by the more distinctly cordate leaves and undulate leaf margins, resembles material known from the present study to be restricted to the northern Yorke Peninsula region and Crystal Brook area. This specimen is almost certainly that referred to in the protologue as having been collected at Crystal Brook. One syntype collection, therefore, is in fact divided so that part is mounted on each of three sheets (AD, BM, MEL) while the other collection consists of a single piece on the AD sheet. The specimen MEL41019 is designated Lectotype; it bears a label in Mueller's hand and is the most ample specimen. It had been labelled (mistakenly in light of the foregoing discussion) as a holotype.

Distribution and Ecology. Known only from South Australia where it occurs in scattered populations at similar latitudes, in three main areas: on northern Eyre Peninsula; northern Yorke Peninsula together with the adjacent northern plains west of the southern Flinders Ranges and northern Mount Lofty Ranges; and east of these ranges, in an area on both sides and in the vicinity of the River Murray (Fig. 3).

Grammosolen dixonii is found almost exclusively on calcareous pale red sandy soils in mallee vegetation and is frequently associated with *Triodia*. It is generally a plant of disturbed sites, which promote seed germination and may be locally frequent following fire. Mechanical damage or burning of the aerial parts may stimulate the production of suckers from the stem base.

Phenology. Flowering specimens have been collected in all months except February, May and June, with most from August to January. Fruiting specimens have been collected from November to January. Galling of fruits as a result of insect attack is a common occurrence.

Conservation status. *Grammosolen dixonii* is relatively rare, with many populations occurring in depleted remnant vegetation on roadsides in agricultural areas. Populations are conserved in several reserves such as the Lake Gilles, Clements Gap, Pooginook and Cooltong Conservation Parks.

Diagnostic features. *Grammosolen dixonii* is clearly distinct from the other species in the genus, on account of its ovate-triangular to sub-cordate leaves and the combination of stalked multangulate-dendritic and verticillately branched hairs on the axes and leaves. There is no intergradation with other species, though in the vicinity of Kyancutta on Eyre Peninsula, populations at the north-western extreme of the range of *G. dixonii* closely approach, within 25 km, populations at the furthest south-eastern extent of the occurrence of *G. truncatus*.

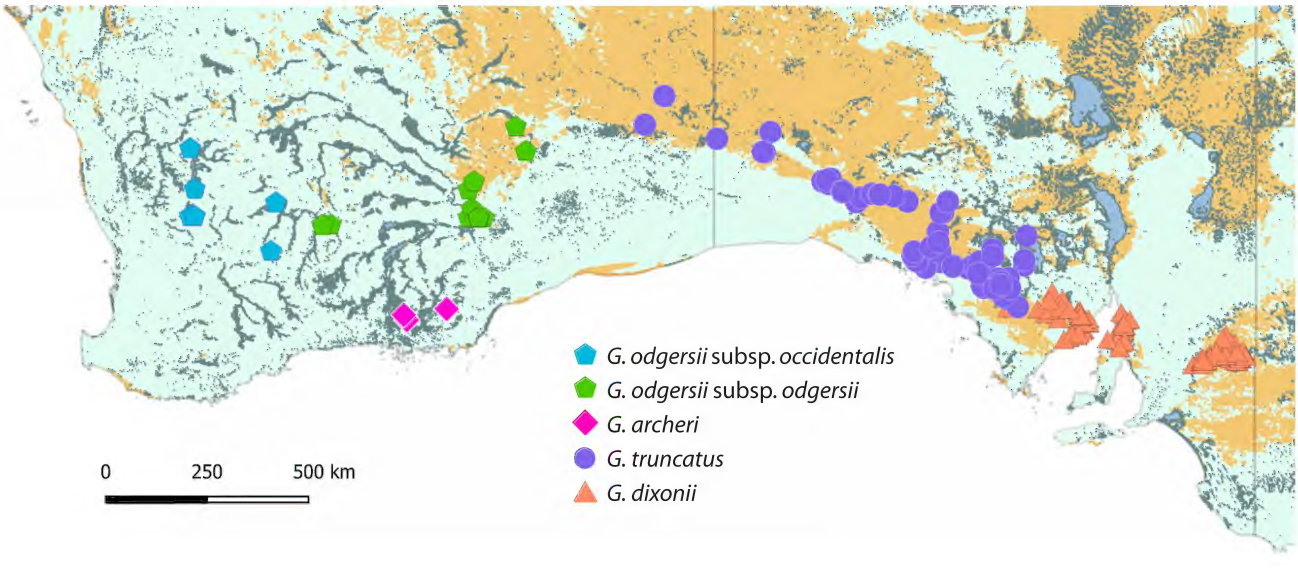

Fig. 3. Southern (central and western) Australia, showing the geographical occurrence of 4 species of *Grammosolen*, including two subspecies (from AVH, ALA–accessed 3 July 2019 and corrected) in relation to extent of sand-ridges (tan) and lakes/drainage systems (grey).

Variation. Plants with acuminate (rather than acute) leaf apices, undulate margins and less dense indumentum predominate in the northern Yorke Peninsula populations; similar specimens are rare elsewhere. Leaves are mostly in the range 8–16 × 6–15 mm, but plants with smaller leaves are found mainly on Eyre Peninsula (e.g. *Orchard 2935*, leaves 7 × 6 mm) while the largest-leaved plants occur on Yorke Peninsula (e.g. *Copley 144*, leaves to 20 × 17 mm). Slight zygomorphy of the corolla is apparent in some plants seen in the fresh state (e.g. *Haegi 1331*, from Northern Lofty Region). Two of the lobes assume an upper, more vertical position and may be slightly closer together, while the remaining three lobes are oriented more horizontally, though not otherwise differently positioned than in regular flowers. There is insufficient correlation of variation in any of these characters either with other characters or geographically for the recognition of any infraspecific taxa.

Derivation of name. Named for Samuel Dixon, an Adelaide geologist and naturalist who had a special interest in fodder plants and collected the type material in the 1880's (see Sharr 1978).

Selected specimens (145 examined)

SOUTH AUSTRALIA. **Eyre Peninsula:** 29.5 km E of Kimba, 4.x.1975, *R.J. Chinnock 2747* (AD); Cook Range, Middleback Ranges, 21.ix.1981, *N.N. Donner 8015* (AD); 60 km SW of Iron Knob on Kimba road, 16.x.1975, *L. Haegi 706* (NSW, AD, SYD); 15 km ENE of Cowell on Mitchellville road, 26.viii.1977, *L. Haegi 1304* (NSW, AD, BRI, CANB); Between Cowell and Arno Bay, 27.xi.1961, *D.N. Kraehenbuehl 528* (AD); Foot of Iron Duke at eastern end of Middleback Range, 29.xii.1970, *A.E. Orchard 2935* (AD, CANB); c. 6 km W of Plank Point, 2.ii.1977, *L.D. Williams 9025* (AD, NSW); 10 km SE of Wudinna, 18.xi.1984, *D.N. Kraehenbuehl 5051* (AD). **Northern Lofty:** Sections 141–150, Hundred of Wiltunga, 13.ii.1966, *B. Copley 34* (AD); Southern boundary of Section 195, Hundred of Wiltunga, c. 140 km NNW of Adelaide, 20.iii.1966, *B. Copley 144* (AD); Mundoora, c. 50 km SSE of Port Pirie, iv.1962, *G. Gardiner s.n.* (AD96323154); 5.7 km S of Wandearah East Post Office on Port Broughton road, 29.viii.1977, *L. Haegi 1331* (NSW, AD, CORD, K, MEL, MO, PERTH); W of Ninnes, which is 120 km NNW of Adelaide, 8.xii.1963, *D.N. Kraehenbuehl 1049* (AD). **Murray:** Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash, 4.ii.2015, *J.R. Guerin 204* (AD); 20 km NE of Blanchetown on Waikerie road, 5.x.1975, *L. Haegi 676* (NSW, AD, BRI, CBG, NT, PERTH); 18 km WSW of Waikerie on Sturt Hwy to Blanchetown, 15.xi.1975, *L. Haegi 868A–J* [population collection documenting variability] (AD, BRI, CANB, HO, MEL, NSW, NT, PERTH); 16 km N of New Well on road running almost due N to main Blanchetown–Waikerie road, 15.xi.1975, *L. Haegi 869* (NSW, AD); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1252* (NSW, AD); 21 km by road NE of Blanchetown on Waikerie road, 17.xi. 1976, *L. Haegi 1263* (NSW, AD); - also 13.x.1977, *L. Haegi 1457G, H, I, L, M, O, P, Q, R, S, T, U, V, W, X, Y* [population collection at site of occurrence of putative hybrid with *Cyphanthera myosotidea*, also documenting variability in *G. dixonii*] (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 26.xii.1978, *L. Haegi 1598* (NSW, AD, BIRM, F, HO); Area between Oak Dam (Frenchs Dam) and Gypsum Hills, c. 32 miles (c. 52 km) N of Overland Corner, 9.x.1965, *D.E. Symon 3627* (AD, CANB, K); 45 km NW of Renmark on road to Canopus Station, 27.ii.1976, *L.D. Williams 7768* (AD); Glossop, between Barmera and Berri, x.1963, *Woolmer 75* (AD). **Yorke Peninsula:** 32 km NW of Port Wakefield, 29.iii.1966, *B. Copley 177* (AD); 8 km WNW of Bute, 15.x.1975, *L. Haegi 705* (AD).

Occurrence of putative intergeneric hybrids involving *G. dixonii*

Several specimens not referable to known species were encountered in small areas where populations of *G. dixonii* overlap with those of species in two other genera of Anthocercideae: *Cyphanthera myosotidea* in one case and *Duboisia hopwoodii* in the other. Closer examination reveals that the specimens are visually intermediate between the two sets of parents, suggesting a hybrid origin for these plants. To test this notion further, specimens of the intermediates and parents from each of the two localities were subjected to simple morphometric analysis and an assessment of pollen fertility.

Pollen viability of samples from both putative parents and the morphologically intermediate specimens was tested. A very low rate of staining was recorded in all intermediates, contrasting with high rates in the putative parents and supporting the assessment of the intermediates as of hybrid origin.

Phytochemical investigations of the leaves of the putative parents and hybrids (El Imam *et al.* 1991) provide further evidence for the hybrid origin of the intermediates; these studies revealed that each of the parents has a unique combination of tropane and pyridine alkaloids and that the alkaloid spectra of each set of morphological intermediates combine those found in the parents. Together these various observations provide strong circumstantial evidence for the intermediates being hybrids. The occurrence of intermediates limited to areas of overlap in the distributions of each of the parents is consistent with this conclusion. In both cases, flowering periods overlap. No manipulated crossing experiments have been performed to demonstrate that hybridisation is possible.

Cyphanthera myosotidea × *Grammosolen dixonii*

A few plants visually intermediate between these two species were encountered along the road verge between 20 and 30 km NE of Blanchetown, South Australia, the only area where the two species are known to be sympatric. Their presence followed major disturbance involving extensive earthworks associated with realignment of the road. Here *G. dixonii* was conspicuous and locally common but *C. myosotidea* was rare. A quantitative assessment of these specimens confirms their intermediacy when compared with material of the two species found at the site (Table 1, Fig. 4). Similarly, pollen fertility was low in a specimen

Table 1. Comparison of certain characters in *Cyphanthera myosotidea*, *Grammosolen dixonii* and a putative hybrid.

Character		*Cyphanthera myosotidea*	Putative hybrid	*Grammosolen dixonii*
Indumentum		Inconspicuous, moderately dense pubescence mainly of simple glandular (with a few eglandular) hairs	Moderately conspicuous, moderately dense tomentum of eglandular branched hairs	Conspicuous, dense tomentum of eglandular branched hairs
Leaf	length (mm)	2–10	8–16	8–16
	breadth (mm)	1–4	3–5	6–15
	shape	Ovate to elliptic or narrowly so	Ovate	Ovate-triangular to very broadly so
	length : breadth	(1.8–) 2.0–6.0 (– 8.0)	2.4–3.5	(0.8–) 0.9–1.5 (– 2.5)
	margins	Flat	Slightly undulate	Undulate
Inflorescence		Flowers scattered in distal parts	Flowers in open leafy spikes	Flowers in dense, leafy spikes
Pedicel		Long, conspicuous	± Short, inconspicuous	Short, inconspicuous
Corolla-lobe	shape	Broadly elliptic	Ovate-elliptic	Ovate to elliptic
	length : breadth	0.8–1.3	1.5–1.7	1.4–2.2
Alkaloid spectrum of leaves (after El Imam *et al.* 1991).		Hyoscyamine or atropine; hyoscine (principal alkaloid); norhyoscyamine or noratropine; 6β-hydroxyhyoscyamine; 3α-tigloyloxytropane; scopine or oscine; tropine; 3-phenylacetoxynortropan-6,7-diol.	Hyoscine; apohyoscine; 6β-hydroxyhyoscyamine (principal alkaloid); tropine; two unidentified bases.	Hyoscyamine; hyoscine; apohyoscine; 3α-acetoxytropane; no particular alkaloid recorded as predominant.

Table 2. Pollen sterility estimates in *Cyphanthera myosotidea*, *Grammosolen dixonii* and a putative hybrid.

	Cyphanthera myosotidea	Putative hybrid	*Grammosolen dixonii*
% sterile pollen	2%	61%	2%
No. of grains counted	183	142	121
Voucher specimen	*Haegi 1262*	*Haegi 1265*	*Haegi 1263*

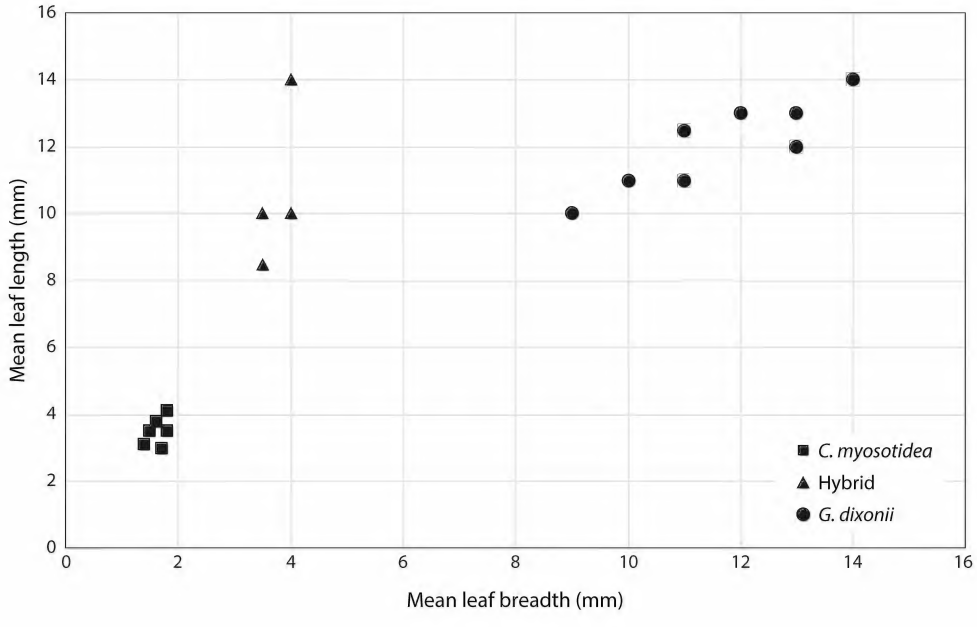

Fig. 4. Scatter plot portraying intermediacy of putative hybrids between *Cyphanthera myosotidea* and *Grammosolen dixonii*, as demonstrated by leaf characters. Each plotted point represents a specimen; four leaves measured per specimen; all specimens from Murray Region, South Australia (cited above and below).

of the intermediate material but high in specimens of the parents from the same site (Table 2). Staining grains in the hybrid were markedly smaller than those of the parents. Observation of meiosis in pollen mother cells of the putative hybrid indicated a high rate of failure in pairing of chromosomes to form bivalents at Metaphase 1, while normal meiosis was observed in the putative parents (see Table 2).

Noting that 6β-hydroxyhyoscyamine, a minor component of *C. myosotidea*, is present as the principal base in the anomalous material and that tropane alkaloid yields of this material are intermediate between those of the two parents, El Imam *et al.* (1991) observe that this is consistent with hybrid origin. They also conclude that hybridisation of these species appears to exert an influence on the capacity of the progeny to convert hyoscyamine into hyoscine, a reaction generally involving 6-hydroxyhyoscyamine as an intermediate.

Specimens seen (all Murray Region, S.A.)

Cyphanthera myosotidea × *Grammosolen dixonii:* c. 13 km S of Waikerie on roadside, 2.ix.1974, *N. Gemmell 293* (AD, MEL); c. 21 km by road NE of Blanchetown bridge on Waikerie road, 17.xi.1976, *L. Haegi 1264 & 1265* (AD); - also 13.x.1977, *L. Haegi 1457A, B, E, J, K, N* [part of population collection, including both parents] (AD); 20 km NE of Blanchetown bridge on Waikerie road, 3.xi.1978, *L. Haegi 1593* (AD); 28 km NE of Blanchetown on Waikerie road, 14.ix.1974, *D.N. Kraehenbuehl 3392* (AD).

Cyphanthera myosotidea: 13 km SSW of Waikerie, 2.ix.1974, *N. Gemmell 297* (AD); c. 21 km by road NE of Blanchetown bridge on Waikerie road, 17.xi.1976, *L. Haegi 1262* (AD); - also 13.x.1977, *L. Haegi 1457C, D, F* [part of population collection, including putative hybrid and both parents] (AD); Waikerie, 15.x.1968, *Miller s.n.* (AD96846176); 61 miles (c. 98 km) SW of Renmark, 18.ix.1967, *B.H.A. Tönnies s.n.* (AD97424250); 16 km WSW of Waikerie, 18.ix.1967, *Wheeler 452* (AD); c. 15 km SW of Waikerie, 26.ix.1971, *D.J.E. Whibley 3618* (AD).

Grammosolen dixonii: see main treatment above.

Duboisia hopwoodii × *Grammosolen dixonii*

Specimens apparently resulting from hybridisation of these species were collected during the 1970's from two sites near Berri and Renmark, c. 200 km NE of Adelaide, South Australia. Both sites have been visited and only a small number of putative hybrids were seen at each. A much more recent collection made in 2015 from a third site in the same area (*Guerin 205*) provides evidence of the intermittent continued recurrence of the hybridisation event. The parents are markedly different from each other in several morphological features (Table 3) and the intermediacy of the hybrid is visually obvious (Figs 2, 5 & 6). The average dimensions of leaves from several specimens collected in the area of occurrence have been plotted to demonstrate this quantitatively (Fig. 7). Pollen from a specimen of putative hybrid origin showed markedly higher sterility than found in either parent (Table 4). A high rate of failure in pairing of chromosomes was observed in pollen mother cells at meiosis, while normal meiosis was observed in the putative parents (see Table 4).

El Imam *et al.* (1991) state that the establishment of nornicotine and hyoscine as the principal alkaloids, together with the co-occurrence of other bases of the parents firmly support the assignment of the intermediate as a hybrid (Table 3).

Specimens of this hybrid were at one time thought to be a new species related to *Cyphanthera albicans* by South Australian botanists. Striking features distinguishing the hybrid from species of the tribe are the glabrescent branches and leaves combined with the undulate margins of the leaves.

Specimens seen

Duboisia hopwoodii × *Grammosolen dixonii:* SOUTH AUSTRALIA. **Murray Region:** 8 km N of Berri, 4.i.1970, *B. Copley 3000* (AD); 8 km N of Berri, 19.xii.1973, *B. Copley 4181* (AD); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1250* (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 26.xii.1978, *L. Haegi 1600 & 1601* (AD); 2 km NE of Stony Pinch Dam, c. 15 km NW of Renmark, 22.iv.1979, *L. Haegi 1773* (AD); sand ridges 3 km W of Stony Pinch (burnt), 5.x.1980, *A.E. Spooner 7265* (AD); Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash 4.ii.2015, *J.R. Guerin 205* (AD).

Duboisia hopwoodii: SOUTH AUSTRALIA. **Murray Region:** c. 128 m N of Renmark, 6.i.1926, *J.B. Cleland s.n.* (AD966030806); c. 10 km N of Berri, 25.viii.1962, *J.B. Cleland s.n.* (AD97217266); Calperum Station, c. 10 km ENE of Berri, 4.i.1970, *B. Copley 2999* (AD); c. 15 km NE of Monash, 22.iv.1957, *H. Eichler 13823* (AD, CANB); 11 km NNE of Berri, 21.x.1976, *L. Haegi 1251* (AD); Canopus Station, c. 185 km ENE of Burra and c. 95 km N of Renmark, 6.viii.1965, *A.C. Robinson 34* (AD); Calperum Station, Overflow Track, at a point c. 20 km NNE of Monash 4.ii.2015, *J.R. Guerin 203* (AD). NEW SOUTH WALES. **South Far Western Plains:** 110 km S of Broken Hill on Wentworth road, 1.ix.1962, *J.B. Cleland s.n.* (AD97217258).

Grammosolen dixonii: see specimens cited under *G. dixonii* above.

2. *Grammosolen truncatus* (Ising) Haegi

Telopea 2(2) (1981) 178. — *Anthotroche truncata* Ising, *Trans. & Proc. Roy. Soc. S. Austral.* 46 (1922) 605, t. 38, 39, Fig. 1. — **Type citation:** "Ooldea, East-West Railway Line, September 15, 1920, and Barton, in the same district, September 19, 1920." **Lectotype (here designated):** Ooldea, Sept. 1920, *Ising 1297* (AD98209191). **Isolectotypes:** AD, BM, BRI, DNA, CANB, K, L, MEL, NSW. **Remaining syntype:** Barton, 19.ix.1920, *Ising 1374* (AD).

Erect, somewhat stiff, grey-green *shrub* 0.7–2 m tall and diam. *Branches* very densely and closely tomentose with multangulate and multangulate-dendritic hairs mostly 0.1–0.2 mm and fewer to 0.25 mm, the indumentum very gradually wearing with age. *Leaves* mostly ± spreading, some in small clusters on much-condensed

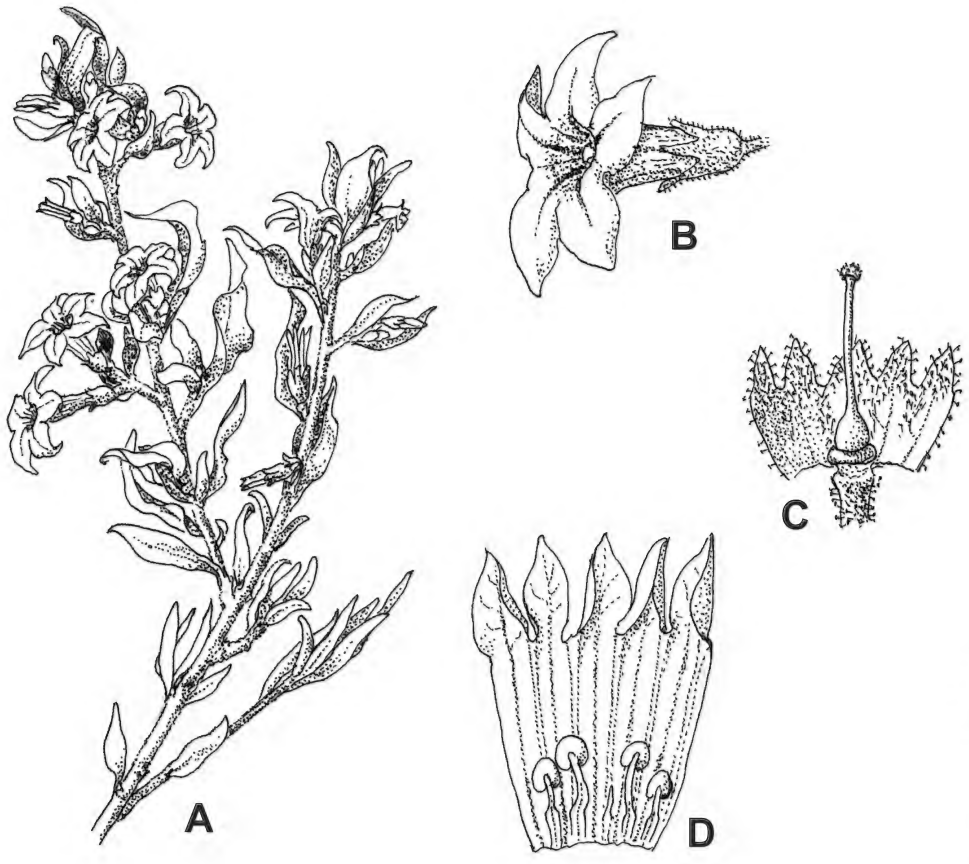

Fig. 5. ***Duboisia hopwoodii* × *Grammosolen dixonii*.** **A** flowering branchlet, × 1; **B** flower, × 3; **C** calyx of advanced bud opened out, with pistil, × 5; **D** opened corolla of same, × 5. (*Haegi 1600*). Illustration by M. Perkins.

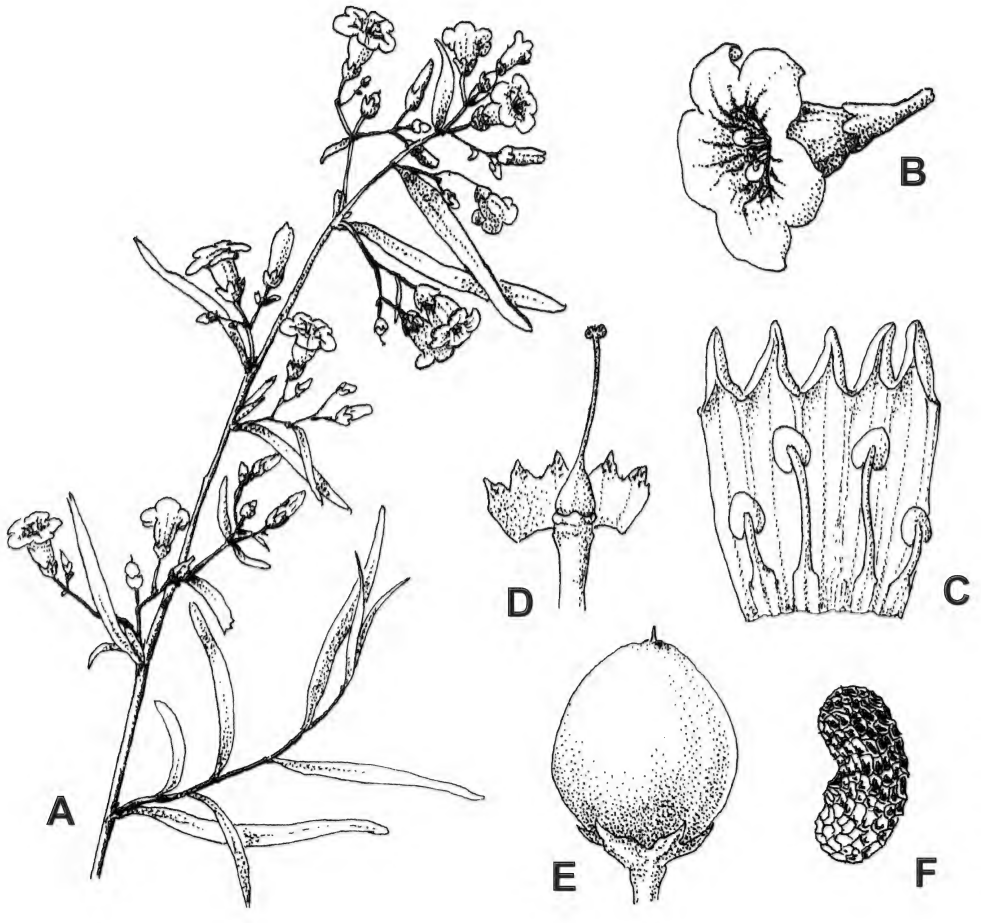

Fig. 6. ***Duboisia hopwoodii*.** **A** flowering branchlet, × 1; **B** flower, × 3; **C** corolla of advanced bud, opened out, × 5; **D** calyx and pistil of same, × 5; **E** berry, × 5; **F** seed, × 10. (*Haegi 888*). Illustration by M. Perkins.

Table 3. Comparison of certain characters in *Duboisia hopwoodii*, *Grammosolen dixonii* and a putative hybrid.

Character		*Duboisia hopwoodii*	Putative hybrid	*Grammosolen dixonii*
Indumentum		Glabrous	Immature parts conspicuously tomentose; mature parts glabrescent	Conspicuous, dense tomentum of eglandular branched hairs
Leaf	length (mm)	35–105	8–16	8–16
	breadth (mm)	2–8	3–5	6–15
	length : breadth	(6–) 10–35 (–71)	2.4–4.5	(0.8–) 0.9–1.5 (–2.5)
	margins	Flat	Undulate	Slightly undulate
Corolla-lobe	shape	Broadly ovate to orbicular	Ovate-elliptic	Ovate to elliptic
	length : breadth	(0.3–) 0.5–1.2	1.5–1.7	1.4–2.2
Stamens		4	4 or 5	5
Alkaloid spectrum of leaves (after El Imam *et al.* 1991).		Hyoscine; nicotine; nornicotine (principal alkaloid); N-acetylnornicotine; N-formylnornicotine.	Hyoscine (2nd major alkaloid); apohyoscine and 3α-acetoxytropane in admixture; nicotine (in hyoscine picrate mother liquor); nornicotine (principal alkaloid); N-formylnornicotine.	Hyoscyamine; hyoscine; apohyoscine; 3α-acetoxytropane; no particular alkaloid recorded as predominant.

Table 4. Pollen sterility estimates in *Duboisia hopwoodii*, *Grammosolen dixonii* and a putative hybrid.

	Duboisia hopwoodii	Putative hybrid	*Grammosolen dixonii*
% sterile pollen	2.8%	86.0%	1.0%
No. of grains counted	545	372	283
Voucher specimen	*Haegi 1599*	*Haegi 1600*	*Haegi 1598*

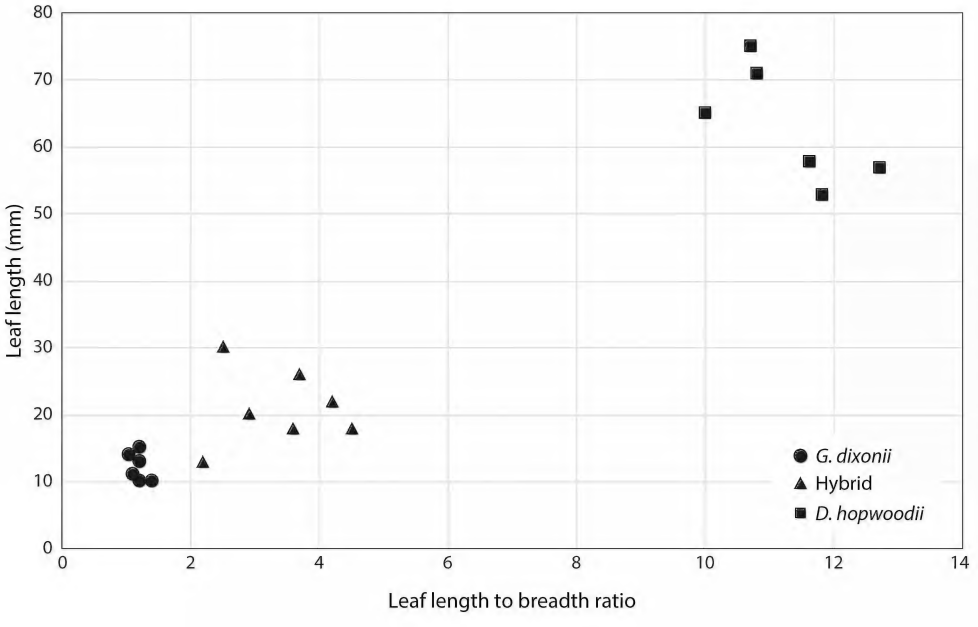

Fig. 7. Scatter plot portraying intermediacy of putative hybrids between *Duboisia hopwoodii* and *Grammosolen dixonii*, as demonstrated by leaf length and leaf length to breadth ratio. Each plotted point represents a specimen; four leaves measured per specimen; all specimens from Murray Region, South Australia or adjacent area in New South Wales (cited above).

axillary branchlets but generally spaced so as not to obscure axis, petiolate; *petiole* 2–4 × 0.5–0.8 mm, tomentose as for lamina; *lamina* ovate to ovate-elliptic, sometimes broadly or narrowly so, less commonly elliptic (L:B 1.1–1.7 (–2.3)), (5–) 7–13 (–18) × (3.5–) 4–10 (–11) mm, very densely and closely tomentose with multangulate and multangulate-dendritic hairs 0.05–0.15 mm above and below; *base* cuneate; *apex* acute to slightly obtuse, blunt; *margin* entire, flat, or often slightly thick or recurved; *midrib* faintly prominent above, prominent, conspicuous and often with visible secondary veins below. *Flowers* borne in short, leafy clusters of one or two, 1–3-flowered cymes on much-condensed lateral branchlets, scarcely aggregated to form leafy spikes; *inflorescence-bracts* 1.5–3 × 0.7–1 mm, moderately tomentose with multangulate-dendritic hairs. *Pedicel* 0.3–0.6 mm, glabrous to moderately pubescent with multangulate-dendritic hairs c. 0.15 mm and glandular hairs 0.1–0.15 mm. *Calyx* 2.5–4 mm, outside very densely tomentose with multangulate-dendritic hairs mostly 0.1–0.2 mm, with fewer c. 0.25 mm, and scattered glandular hairs 0.1–0.15 mm, inside moderately pubescent with antrorse glandular hairs, 0.08–0.15 mm, especially on the lobes; *calyx-lobes* acute to slightly obtuse, angular or blunt, 0.2–0.4 times as long as tube, 0.5–1 × 1–1.2 mm, sinuses obtuse. *Corolla* (7.3–) 9.5–11 mm, ± dull-white with violet striations, outside moderately to densely pubescent with multangulate and forked hairs 0.2–0.25 mm on lobes and upper tube, inside very densely papillose with hairs 0.1–0.2 mm on lobes; *tube* 4.5–6.3 mm, markedly widening in upper 0.5–1 mm, diam. 1.3–1.8 mm at base and 2.8–3.5 mm at limb base; *lobes* elliptic to ovate with truncate base (L:B 1.7–2.4), (2.5–) 3.5–6 × (1.5–) 2.0–2.8 mm, sometimes slightly narrowed at the base, apex rounded to bluntly acute, margin flat. *Stamens* 5, 3–4 mm and 2–3.2 mm; *filament-bases* densely pubescent with simple, forked and sparingly branched hairs, 0.2–0.25 mm, less dense abaxially; *anthers* c. 0.8 × 1.0 mm. *Ovary* globose to depressed globose, 0.8–1 × 0.8–1.1 mm; *ovules* 5–10 in total; *style* 2.9–4 mm, ± equal to the longer stamens and included by 0.5–1 mm; *disc* undulate, 0.3–0.5 mm high, usually slightly, rarely much greater in diameter than ovary (to 1.5 mm), red. *Capsule* somewhat inconspicuous, partly embedded in hairs of enclosing calyx, axis and leaves, globose, 4–4.5 mm diam. *Seeds* c. 4, c. 2.8 × 1.2 mm; *surface-reticulae* 0.1–0.25 × 0.1–0.25 mm. *Chromosome number:* n=56 (*Haegi 1597*). **Fig. 8.**

Distribution and Ecology. *Grammosolen truncatus* occurs in South Australia and Western Australia, extending from north-west Eyre Peninsula and the western Gawler Ranges north-west into the southern Great Victoria Desert. It is always found on deep sandy soils, commonly on sand dunes or localised sandy rises. It is primarily a plant of burnt or otherwise disturbed sites in mallee vegetation, sometimes associated with *Callitris* and seems to occur mainly in small scattered populations. See *G. dixonii* above for comments on the co-occurrence of these two species on Eyre Peninsula (Fig. 3).

Phenology. Flowering specimens have been collected from August through February but the main flowering season appears to be in September and October. Fruiting specimens have been collected in September, October and January. Data are unavailable for the months March to July.

Conservation status. *Grammosolen truncatus* is an uncommon plant known from only about 70 collections. It is not recorded from any conservation reserves.

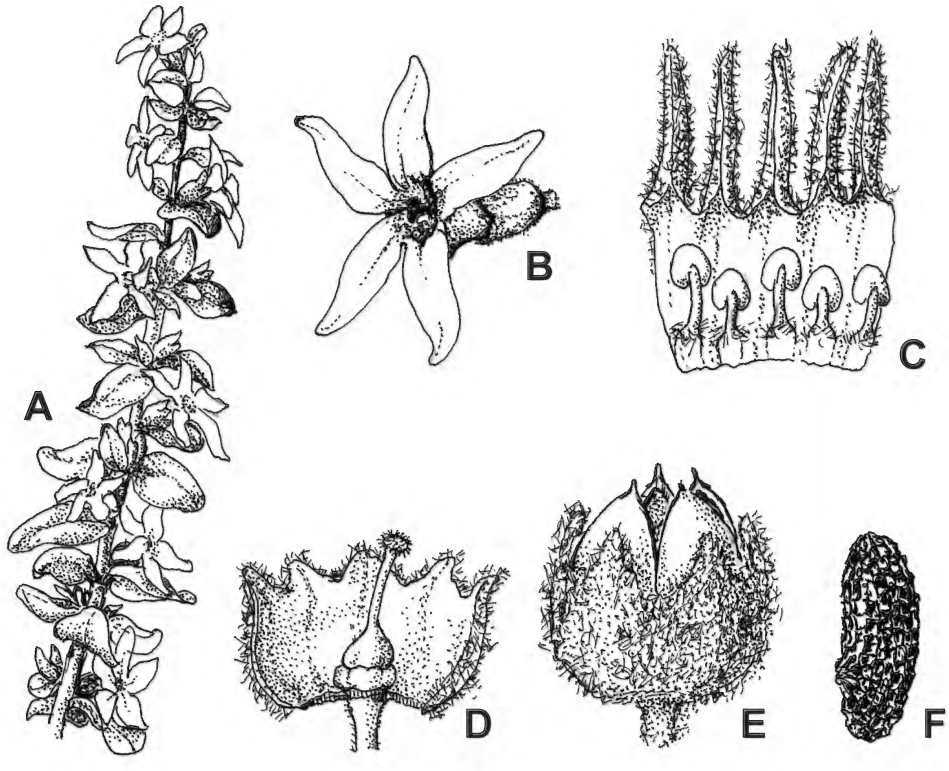

Fig. 8. *Grammosolen truncatus*. A flowering branchlet, × 1; **B** flower, × 2.5; **C** corolla of advanced bud, opened out, × 6; **D** opened calyx and pistil of same, × 6; **E** capsule, × 6; **F** seed, × 10. (*Haegi 770*). Illustration by M. Perkins.

Diagnostic features. *Grammosolen truncatus* is clearly related to *G. dixonii* and *G. archeri* but is perhaps closer to *G. archeri*. The western extremity of the range of *G. dixonii* almost meets but does not overlap with the eastern extent of the occurrence of *G. truncatus*, while *G. archeri* has a distinct geographical range separated by several hundred kilometres from both other species.

Variation. *Grammosolen truncatus* is relatively uniform throughout its range, with both the smallest-leaved specimens (e.g. *Symon 8120*, *Blaylock 2035*) and the largest-leaved ones (e.g. *Haegi 770*) occurring in the Gawler Ranges populations.

Hybrids. None recorded.

Derivation of name. From the Latin *truncatus*, truncate, in reference to the shortly lobed calyx, as indicated in the protologue.

Notes. Some details in the protologue description have not been substantiated in this study. My observations indicate that the hairs of the indumentum are not "plumose" but multangulate-dendritic; the stamens are included, not "scarcely exsert" and the ovary is glabrous, not "with a few stellate hairs". Examination of the greater number of specimens now available indicates that up to four seeds develop: in Ising's material the capsules were one-seeded.

Selected specimens (70 examined)

WESTERN AUSTRALIA. **Great Victoria Desert IBRA Region:** Anne Beadell Highway, 37 km E by track of Ilkurkla roadhouse, 6.x.2010, *R. Davis, J. Jackson & D. Ferguson 11636* (PERTH, CANB *n.v.*). SOUTH AUSTRALIA. **North Western:** c. 135 km N of Cook, just in main dunes, 18.viii.1980, *D.E. Symon 12233* (AD, NSW). **Nullarbor:** 2 miles [c. 3 km] S of Maralinga on sand ridge, 10.x.1956, *N. Forde 620* (AD, CANB); 35 km E of Barton on Transcontinental Railway, 24.x.1970, *B. Lay 81* (AD, MEL). **Gairdner Torrens:** 15 km S of Lake Everard Homestead, 20.ix.1972, *J.Z. Weber 3202* (AD). **Eyre Peninsula:** 30 km NW of Ceduna, 2 km NW of Koonibba Hill, 4.i.1979, *M.D. Crisp 4756* (CBG, AD, NSW); 60 km NNE of Minnipa on Yardea road, 18.x.1975, *L. Haegi 770* (AD, CBG, NSW); 17 km SSW of Hiltaba on Yantanabie road, 19.x.1975, *L. Haegi 775* (AD, BIRM, BRI); 20 km N of Karcultaby, 20.x.1975, *L. Haegi 794* (AD, CORD, MO); c. 29 km by road SW of Yardea Homestead on Minnipa road, 29.x.1978, *L. Haegi 1597* (NSW, AD, CANB, F, HO); 12.4 km directly SSE of Mt. Stuart, 11.x.1999, *D.E. Murfet & R. Taplin 19991011* (AD); 2.9 km directly SSW of Corabinnie Hill, 19.x.2001, *S.D. Kenny BS 128-276* (AD168685).

3. *Grammosolen archeri* Haegi, *sp. nov.*

Grammosolen sp. Mt Ridley (*W.R. Archer 1210911*) W. Austral. Herb., *FloraBase—the Western Australian Flora* (1998–), https://florabase.dpaw.wa.gov.au/ [accessed 5 June 2019]; CHAH, *Austral. Pl. Cens.* (2006), https://biodiversity.org.au/nsl/services [accessed 5 June 2019]. — **Holotype:** Western Australia, Eastern Mallee IBRA subregion, [Vicinity of] Lake Halbert [precise locality details withheld for conservation reasons], 8 Oct. 1990, *W.R. Archer 510907* (PERTH). **Isotypes:** AD, BM, CANB, MEL, MO, to be distributed.

Spreading grey-green *shrub*, 0.6–1 m tall and up to 2 m diam. *Branches* very densely and closely tomentose with multangulate and multangulate-dendritic hairs, mostly c. 0.2 mm and fewer to 0.25 mm, the indumentum gradually wearing off with age. *Leaves* mostly ± spreading, some at times in small clusters on much condensed axillary branchlets but generally spaced so as not to obscure the axis, petiolate; *petiole* 0.4–2.2 × 0.4–0.7 mm, tomentose as for lamina; *lamina* orbicular-reniform to obcordate, sometimes broadly ovate at the shoot tips (L:B 0.65–0.96 (–1.1)), 2.5–7 × 2.6–10 mm, very densely and closely tomentose with multangulate and stalked multangulate-dendritic hairs, 0.1–0.15 mm above and below; *base* usually truncate or shallowly cordate, sometimes broadly cuneate; *apex* bluntly obtuse to rounded; *margin* flat, sometimes thick or slightly recurved; *midrib* obscure adaxially, ± prominent abaxially, sometimes with secondary veins. *Flowers* borne in 1–2-flowered cymes in the distal leaf axils of short or elongate branchlets, scarcely aggregated to form leafy spikes; *inflorescence-bracts* 0.4–0.6 × 0.1–0.2 mm, densely tomentose with multangulate-dendritic hairs. *Pedicel* 0.3–0.5 mm, pubescent with multangulate-dendritic hairs c. 0.15 mm, glandular hairs absent. *Calyx* 2.0–2.5 mm, outside very densely tomentose with multangulate-dendritic hairs mostly 0.1–0.2 mm and fewer to 0.25 mm, inside moderately pubescent with antrorse glandular hairs 0.06–0.1 mm, especially on the lobes; *calyx-lobes* acute, blunt, 0.4–0.5 times as long as tube, 1 × 0.8 mm, sinuses acute. *Corolla* 5.5–6 mm, dull white, striations not recorded, outside moderately to densely pubescent with multangulate and forked hairs 0.15–0.25 mm on the lobes and upper tube, inside very densely papillose with hairs 0.08–0.1 mm on lobes; *tube* 3.5–4 mm long, markedly widened in upper 0.5 mm, diam. 1.2–1.4 mm at base, and 2.0–2.4 mm at limb-base; *lobes* ovate-elliptic with truncate base, (L:B 1.7–1.8), 2.0–2.5 × 1.2–1.4 mm, sometimes slightly narrowed at base, apex rounded to bluntly obtuse, margin flat. *Stamens* 5, the longer ones 3.0–3.3 mm and the shorter ones 2.5–2.7 mm; *filament-bases* densely pubescent with simple, forked and sparingly-branched eglandular hairs 0.2–0.3 mm, equally dense abaxially; *upper anthers* c. 0.5 × 0.6 mm, *lower anthers* sometimes slightly smaller, 0.4–0.5 × 0.5–0.6 mm. *Ovary* globose, 0.6 mm diam.; *ovules* 6–8 in total; *style* 1.9–2.1 mm, ± equal to the longer stamens and included by 0.5 mm; *stigma* c. 0.15 × 0.3 mm; *disc* undulate, 0.2–0.3 mm high, c. 0.8 mm diam., colour and consistency unknown. *Capsule* ± inconspicuous, largely enclosed by the tomentose calyx, globose, 2.5–3.0 mm diam. *Seeds* 3–4, c. 2.2 × 1.2 mm; surface-reticulae 0.1–0.15 × 0.05–0.15 mm. *Chromosome number* not determined. **Fig. 9.**

Distribution and Ecology. Endemic to Western Australia where it is to date known only from the Eastern Mallee IBRA subregion in the South Western Province, in an area 70–90 km inland from the coast between Esperance and Cape Arid. The three known

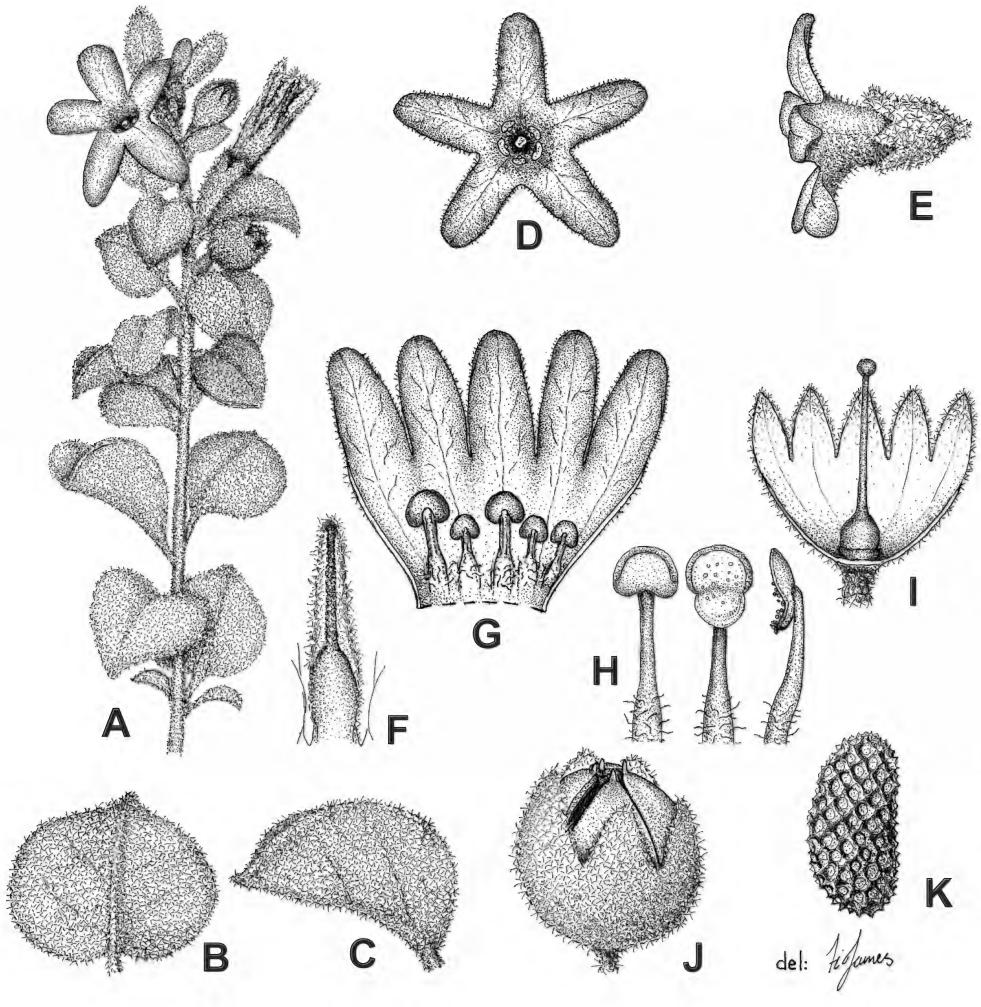

Fig. 9. *Grammosolen archeri*. **A** flowering branchlet, × 4.5; **B** leaf, spread, upper side, × 7.5; **C** leaf showing orientation and underside, × 7.5; **D** flower from above, × 6; **E** flower from side, × 6; **F** corolla lobe, late bud stage, × 12; **G** corolla opened out, with androecium, × 7.5; **H** stamens showing adaxial dehiscence, × 19; **I** calyx opened out, with pistil, × 9; **J** capsule, × 7.5; **K** seed, × 11. (*W.R. Archer 2909916*). Illustration by F. James.

populations occur below 200 m altitude in the 300 mm to 400 mm mean annual rainfall zone, on disturbed sites in deep sandy loam soil and in mallee-heath vegetation (Fig. 3).

Conservation status. Rare and poorly known. Listed under the schedules of the Western Australian Wildlife Conservation (Rare Flora) Notice as a Priority 1 species, reflecting inadequate knowledge of its occurrence and abundance, because of the small number of collections and relatively poorly collected area it occurs in.

Diagnostic features. *Grammosolen archeri* differs from all three other species in its distinctive, small, orbicular-reniform to obcordate leaves and in its much smaller flowers and fruits. It seems closest to *G. truncatus* and, perhaps somewhat less so, to *G. dixonii*. It is of similar appearance, with a dense covering of multangulate and multangulate-dendritic hairs on vegetative parts and with flowers of very similar appearance (dull white corolla with ovate-elliptic lobes; the occurrence of striations in the tube is expected but yet to be observed). Like *G. dixonii* it has a spreading habit and subsessile leaves, while it is similar to *G. truncatus* in being more openly branched and having small inflorescences borne on short lateral shoots (though these are sometimes elongate in *G. archeri*). In *G. dixonii* the leaves are usually closely spaced so as to be overlapping, concealing the axis (especially in the more distal parts), and with flowers aggregated into leafy spikes. From *G. odgersii* it differs in having five (cf. four) fertile stamens and in lacking verticillately-branched hairs on the vegetative parts.

Variation. No appreciable patterns of variation are evident in *G. archeri*, which is recorded from only three collections across an area about 100 × 20 km.

Derivation of name. Named for William R. Archer, botanical collector and horticulturist of Esperance, Western Australia, who first discovered this species in the field and has collected the only known material of it.

Specimens seen (precise locality details withheld for conservation reasons)

WESTERN AUSTRALIA. **Eastern Mallee IBRA subregion:** [Vicinity of] Lake Halbert, 17 Feb. 1990, *W. Archer 1702903* (AD; PERTH, to be distributed); 12.x.1991, *W.R. Archer 1210911* (MEL; also PERTH, HO *n.v.*); [Vicinity of] Mt Ridley, 13.x.1990, *W.R. Archer 13109010* (AD; PERTH, BRI, BM, to be distributed); [Vicinity of] Mt Buraminya, 29.ix.1991, *W.R. Archer 2909916* (AD; CANB, MEL *n.v.*; K, NSW, PERTH, to be distributed).

4. *Grammosolen odgersii* (F.Muell.) Haegi, *comb. nov.*
Anthocercis odgersii F.Muell., *Fragm.* 10 (1876) 19; C.A.Gardner, *Enum. Pl. Austral. Occ.*, Part 3 (1931) 116; Beard, *Descr. Cat. W. Austral. Pl.* (1965) 95; J.W.Green, *Cens. Vasc. Pl. W. Austral.* (1981) 92. — *Cyphanthera odgersii* (F.Muell.) Haegi, *Telopea* 2 (1981) 177; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 27. — **Type citation:** "Ad fontes Victoriae; Young". **Lectotype (here designated):** Victoria Spring [Queen Victoria Spring, Western Australia, 30°26'S 123°24'E], *s.dat.*, *Young s.n.* (MEL70945). **Isolectotype:** MEL70234.

Grey-green soft *shrub* 0.5–2.5 m high with ascending or radiating, often arched branches. *Branches* very densely lanate-tomentose with verticillately branched eglandular hairs 0.3–6.5 mm long and scattered simple glandular hairs 0.25–0.5 mm. *Leaves* ± scattered or often crowded towards the ends of branches, spreading, subsessile; *lamina* broadly to narrowly ovate-elliptic (L:B 1.1–3.8), (11–) 12–30 (–35) × 7–13 mm, very densely lanate-tomentose above and below with verticillately branched hairs 0.3–1.0 mm; *base* cuneate to attenuate; *apex* acute and blunt to obtuse or rounded; *margin* flat, rarely slightly inrolled or undulate; *midrib* obscure above and below. *Flowers* in dense axillary and terminal clusters, often forming leafy spikes; *upper inflorescence-bracts* to 5 mm, narrowly elliptic, moderately pubescent adaxially with oblique to antrorse glandular hairs 0.05–0.25 mm, and densely lanate-tomentose abaxially (and also near the apex adaxially) with verticillately branched hairs 0.5–2 mm. *Pedicel* 0.5–2 mm, sparsely to moderately pubescent with simple glandular hairs 0.05–0.75 mm. *Calyx* 4–7 mm, pubescent outside in lower half as for pedicel, in upper half very densely lanate-tomentose with porrect to oblique verticillately branched hairs 0.5–2.5 mm, often entirely obscuring calyx, pubescent inside with porrect to antrorse glandular hairs 0.05–0.25 mm; *calyx-lobes* 2–3 × 1.0–1.7 mm, acute to acuminate, blunt, sinuses acute, angular. *Corolla* 5.5–8.5 mm, white with violet striations, sparsely pubescent outside with glandular hairs 0.05–0.2 mm, very densely pubescent inside with papillae 0.05–0.1 mm; *tube* 4.2–6.5 mm, diam. 0.8–1.5 mm at base and 2.5–4 mm at limb base; *lobes* ovate to broadly ovate with truncate base (L:B 1.1–2.3), 1.3–2.5 × 1.1–1.6 mm, fused for 0.5–1 mm at base, apex rounded, margin flat but whole lobe often somewhat concave. *Stamens* 4, the upper ones 2.0–3.0 mm and the lower ones 1.3–2.2 mm; *filament-bases* pubescent with simple and forked or dendritic eglandular hairs 0.1–0.5 mm and sometimes glandular hairs 0.05–0.15 mm; *anthers* c. 0.8 × 1 mm. *Ovary* ovoid, 0.6–1.6 × 0.5–1.2 mm; *ovules* 5–6 in total; style 2.5–3 mm; *stigma* 0.2–0.3 × 0.3–0.4 mm; disc even to slightly undulate, 0.1–0.3 mm high, bright red. *Capsule* inconspicuous, embedded in dense, long hairs of calyx and axis, ellipsoid to ovoid or broadly so, 3–5 × 2–4 mm. *Seeds* 1–4, 2.8–3.4 × 1.1–1.4 mm; *surface reticulae* 0.2–0.4 × 0.2–0.3 mm. *Gametic chromosome number:* n=30 (*Chinnock 3100*). **Figs 10 & 11.**

Distribution and Ecology. *Grammosolen odgersii* is endemic to southern inland Western Australia where it occurs in a few widely scattered populations in the Avon Wheatbelt and Coolgardie IBRA regions. The range falls entirely within the 150 mm to 500 mm mean annual rainfall zone (Fig. 3).

Conservation Status. See subspecies below.

Diagnostic features. *Grammosolen odgersii* is readily distinguishable from all the other three species in the genus in having flowers with only four (not five) fertile stamens, and in the indumentum on the vegetative parts consisting of very long verticillately branched hairs, up to 6.5 mm long on the axes and up to 1 mm long on the leaves (cf. multangulate and multangulate-dendritic hairs no more than 0.25 mm long in *G. truncatus* and *G. archeri* and a mixture of multangulate-dendritic and verticillately branched hairs no more than 1.5 mm long in *G. dixonii*). *Grammosolen odgersii* is perhaps closest to *G. dixonii* but differs further from it in leaf-shape: broadly to narrowly ovate-elliptic (L:B 1.1–3.8), cf. ovate-triangular to very broadly so, sometimes subcordate (L:B (0.8–) 0.9–1.5 (–2.5)) in *G. dixonii*.

Variation. Although *G. odgersii* is known from fewer than 30 collections, a geographically correlated, bimodal pattern of variation is evident, based on several characters (Table 5). Plants from four populations at the western end of the distribution differ from all other populations mainly in having longer, proportionally narrower leaves, a longer indumentum and shorter corolla-lobes. These have been recognised as subsp. *occidentalis* (Haegi 1981). There are no overlaps in the distributions of the two subspecies and although subsp. *odgersii* has a wide east-west occurrence, there is no perceptible gradation towards subsp. *occidentalis*.

Derivation of name. Named in honour of William Henry Odgers (1828–1881), an under-secretary of the Victorian Chief Secretary's Department, who supported Ferdinand von Mueller (the author of the name) in his cause of carrying out botanical research as an officer of the Victorian Government (see protologue, cited above; Sharr 1978).

Vernacular name. Woolly anthocercis (Grieve & Blackall 1975); woolly cyphanthera (Canackle & Moore 2014).

Key to subspecies of *G. odgersii*

1. Leaves with L:B of 1.1–2.0 and 20 mm or less in length; corolla lobes 2.0–2.5 mm . . . . . **4a.** subsp. ***odgersii***

1: Leaves with L:B of 2.3–3.8 and 18–35 mm in length; corolla lobes 1.3–1.8 mm. . . .**4b.** subsp. ***occidentalis***

Table 5. Morphological differences between the two subspecies of *G. odgersii*.

Character	subsp. *odgersii*	subsp. *occidentalis*
Habit	Low shrub 0.5–1m	Shrub 1–2.5 m
Length of indumentum	0.2–2.0 mm	0.5–3.0 mm
Length to breadth ratio of leaves	(1.1–) 1.4–1.8 (–2.0)	(2.3–) 2.5–3.3 (–3.8)
Leaf length	11–20 mm	18–35 mm
Pedicel length	0.5–1.5 mm	0.9–2.0 mm
Corolla-lobe length	2.0–2.5 mm	1.3–1.8 mm
Pubescence at filament bases	Simple glandular and eglandular hairs	Simple and dendritic eglandular hairs

4a. *Grammosolen odgersii* subsp. *odgersii*

Anthocercis odgersii F.Muell.: F.Muell., *Syst. Cens. Austral. Pl.* (1882) 96; F.Muell., *Second Syst. Census. Austral. Pl.* (1889) 163 (where distribution given erroneously as Northern Australia ("N.A."); Ewart, *Vict. Naturalist* 23(9) (1907) 155, p.p. excluding Cowcowing material; Ewart, *Vict. Naturalist* 24(1) (1907) 12–13, p.p. excluding Koch specimen; Ewart, *Vict. Naturalist* 24(6) (1907) 56, p.p. as to Victoria Springs material; B.J.Grieve & W.E.Blackall, *How to Know W.A. Wildfl.* 4 (1975) 610, [110], p.p., as to "Leaves orbicular-ovate" and ref. to Coolgardie District.

Cyphanthera odgersii (F.Muell.) Haegi subsp. *odgersii*, *Telopea* 2 (1981) 177.

Chloanthes drummondii R.Helms ex Ewart, *Vict. Naturalist* 24 (1907) 12, as '*drummondi*', *nom. inval.*

Shrub 0.5–1 m high with radiating often arched branches. *Branch-indumentum* 0.3–2.0 mm. *Leaf-lamina* ovate-elliptic to broadly so (L:B 1.3–2.2), 11–20 × 7–11 mm, with indumentum 0.3–0.9 mm. *Corolla-lobes* ovate to broadly ovate (L:B 1.3–2.3), 2.0–2.5 × 1.0–1.5 mm. *Filament-bases* pubescent with simple eglandular and glandular hairs. *Gametic chromosome number* n=30 (*Chinnock 3100*). **Fig. 10.**

Distribution and ecology. Subspecies *odgersii* occurs in Western Australia over a wide area from the far western Great Victoria Desert westwards to near Southern Cross, in the 150 mm to 500 mm rainfall zone. It is a rarely encountered plant which occurs in widely scattered populations on open sites in mallee, on sand dunes and sandplain, often following fire. Flowering has been recorded from August to October and fruiting in September and October (Fig. 3).

Conservation status. Uncommon to rare but not threatened.

Variation. Little variation is evident among the small number of specimens of this species collected.

Specimens seen (all cited)

WESTERN AUSTRALIA. **Coolgardie IBRA Region:** Victoria Desert, Camp 58, Elder Exploring Expedition, 25 km NE of Streich Mound, 21.ix.1891, *R. Helms s.n.* (AD96414102, AD97604848, MEL70235, MEL70946, NSW123728, NSW123729); 35 km W of Plumridge Lakes, 8.5 km WNW of Salt Creek airstrip, 15.ix.1979, *J. Taylor 498, M. Crisp & R. Jackson* (CBG, NSW); 89.9 km WSW of Coolgardie, just E of Boorabbin, 18.ix.1976, *R.J. Chinnock 3098, 3099 & 3100* (AD); 82.8 km WSW of Coolgardie, near Boondi, 18.viii.1977, *R.J. Chinnock 3674* (AD); 20.5 km E of Zanthus along Transcontinental Railway line, 17.ix.1979, *M.D. Crisp 5881, J. Taylor & R. Jackson* (PERTH; CBG, NSW *n.v.*); c. 90 km by road SW of Coolgardie on Great Eastern Highway, 4.vii.1979, *L. Haegi 1780* (NSW, BRI, F, PERTH); Near Warangering, Camp 81, Elder Exploring Expedition, 14.xi.1891, *R. Helms s.n.* (AD96414101, AD96430080, MEL70236); Goddard (now Ponton) Creek E of Zanthus, 3.x.1956, *R.D. Royce 5570* (PERTH); 20 km E of Zanthus, 2.ix.1968, *P.G. Wilson 7629* (PERTH, AD); 20.5 km E of Zanthus at Goddard (now Ponton) Creek, 9.xi.1976, *E. Wittwer 1977* (PERTH).

4b. *Grammosolen odgersii* subsp. *occidentalis* (Haegi) Haegi, comb. nov.

Cyphanthera odgersii (F.Muell.) Haegi subsp. *occidentalis* Haegi, *Telopea* 2 (1981) 178; R.W.Purdie, Symon & Haegi, *Fl. Austral.* 29 (1982) 28. — **Type:** "Western Australia, Avon District" [precise locality details withheld for conservation reasons], 23.ix.1976, *L. Haegi 1100*. **Holotype:** PERTH. **Isotypes:** AD, CANB, K, MO.

Anthocercis odgersii F.Muell.: Ewart, *Vict. Naturalist* 23(9) (1907) 155, p.p. as to Cowcowing material; Ewart, *Vict. Naturalist* 24(1) (1907) 12–13, p.p. as to Koch specimen; Ewart, *Vict. Naturalist* 24(6) (1907) 56, p.p. as to Koch specimen; B.J.Grieve & W.E.Blackall, *How to know W.A. Wildfl.* 4 (1975) 610, [110], p.p. as to "linear-oblong", illustration and reference to Avon District.

Erect *shrub* 1–2.5 m high with ascending branches. *Branch indumentum* 1.0–6.5 mm. *Leaf-lamina* ovate-elliptic to narrowly so (L:B 2.3–3.8), 18–35 ×

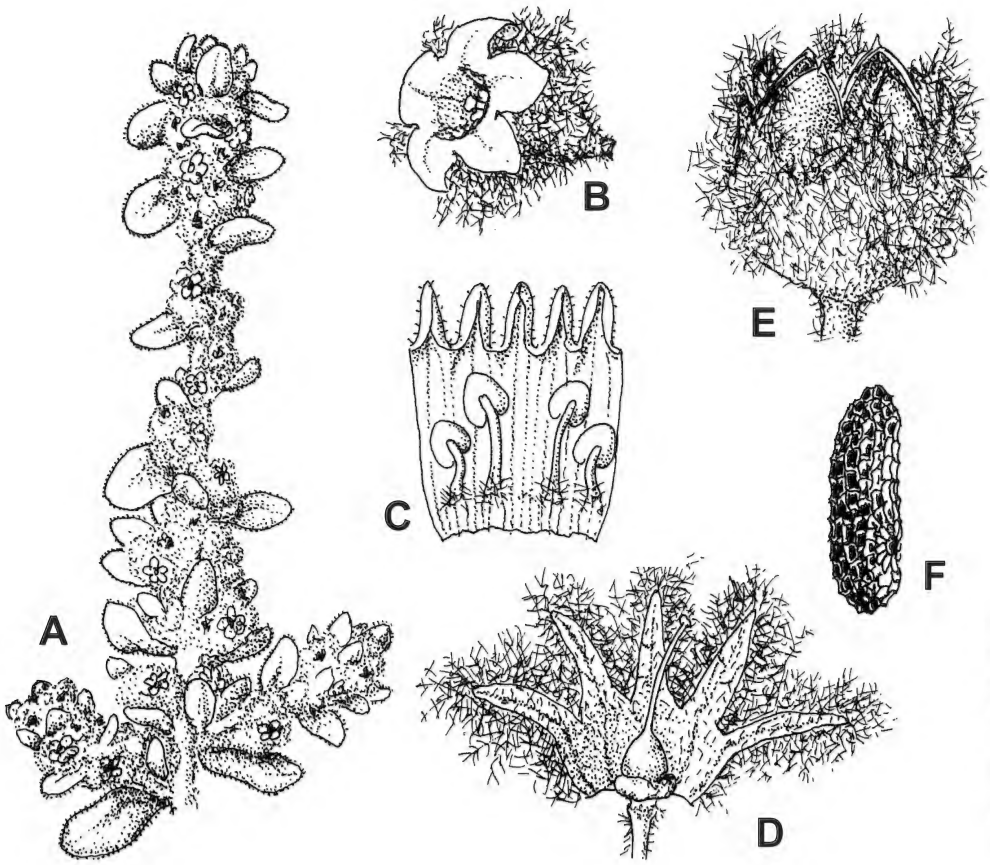

Fig. 10. *Grammosolen odgersii* subsp. *odgersii*. **A** flowering branchlet, × 1; **B** flower, × 3; **C** corolla of advanced bud opened out, × 5; **D** opened calyx and pistil of same, × 5; **E** capsule, × 5; **F** seed, × 10. (*Chinnock 3100*). Illustration by M. Perkins.

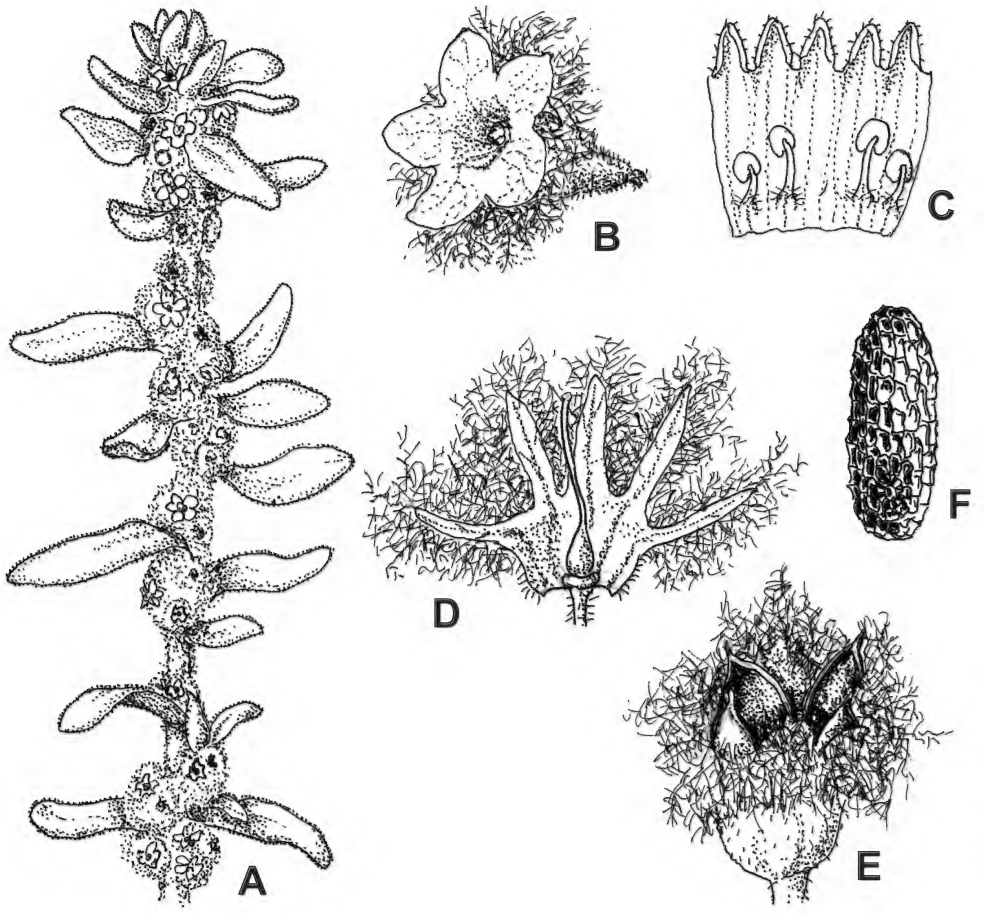

Fig. 11. *Grammosolen odgersii* subsp. *occidentalis*. **A** flowering branchlet, × 1; **B** flower, × 4; **C** corolla of advanced bud opened out, × 5; **D** opened calyx and pistil of same, × 5; **E** capsule, × 5; **F** seed, × 10. (*Haegi 1100*). Illustration by M. Perkins.

8–13 mm, with indumentum 0.5–1.0 mm. *Corolla-lobes* broadly ovate (L:B 1.1–1.5), 1.3–1.8 × 1.0–1.6 mm. *Filament-bases* pubescent with eglandular hairs only. *Chromosome number* not determined. **Fig. 11.**

Distribution and ecology. *Grammosolen odgersii* subsp. *occidentalis* is known from a few small, scattered populations in the Avon Wheatbelt and adjacent Coolgardie IBRA regions in Western Australia, in association with salt lakes forming parts of ancient shallow drainage systems. Plants occur in deep sandy to sandy loam soils, often on disturbed sites (e.g. following fire) in mallee/woodland (Fig. 3).

Conservation status. Listed in Western Australia, (as *Cyphanthera odgersii* subsp. *occidentalis*), applying international criteria, as *Critically Endangered*. For this reason only generalised locality information is provided here. *Grammosolen odgersii* subsp. *occidentalis* has been the subject of intensive recovery work protecting existing populations, propagation of plants for translocation and collection of seed for long-term germplasm storage (Canackle & Moore 2014).

Variation. Little variation is evident among the small number of specimens of this species collected.

Specimens seen (all cited — precise locality details withheld for conservation reasons)

WESTERN AUSTRALIA. **Avon Wheatbelt IBRA Region:** Sep. 1904, *M. Koch s.n.* (no. 1104) (AD, K, MEL70237, MEL70238, MEL70944, NSW, PERTH); Oct. 1939, *C. Gardner s.n.* (PERTH); 3.xii.1946, *C. Gardner 8507* (PERTH); 19.x.1990, *F.H. & M.P. Mollemans 3470* (PERTH); 28.x.1997, *J.A. Cochrane 2460* (PERTH); 12.ix.2007, *J.M. Collins 280* (PERTH); 12.ix.2007, *L. Duffy LD140* (PERTH). **Coolgardie IBRA Region:** June 1990, *F.H. & M.P. Mollemans 2981* (AD, PERTH); 13.ix.1990, *F.H. & M.P. Mollemans 3114* (AD, PERTH).

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The study described here commenced while the author was employed at the Waite Agricultural Research institute, University of Adelaide during 1976 and 1977 and a PhD student at Flinders University of South Australia (1977–1983). The work continued at the National Herbarium of New South Wales (1977–1982) and then at the Botanic Gardens of Adelaide (from 1982). During this time it was supported by grants from the Australian Biological Resources Study, for which I record my gratitude. After a considerable dormancy the work recently recommenced in Adelaide and I thank the Board of the Botanic Gardens and State Herbarium of South Australia for this opportunity, made possible by the support I receive as an Honorary Research Associate. My thanks go to my colleagues at all the institutions mentioned including my PhD supervisor Bryan Barlow, but in particular the late David Symon, not only a supervisor but also a mentor and wise friend. Jim Armstrong, the late Don McGillivray and Jocelyn Powell (Sydney), Philip Short (Melbourne) and Bob Chinnock, Bill Barker, Robyn Barker and Ed Biffin (Adelaide) are sincerely thanked for their beneficial discussions and in some cases assistance in the field. Likewise, I acknowledge provision of several helpful suggestions by an anonymous referee – these have been incorporated in an amended version of the paper. Kathy Stephens and Marie Taylor (Sydney) provided excellent technical assistance; Margaret Perkins and Rob Roden prepared most of the drawings while temporarily employed at the National Herbarium of New South Wales. Fiona James, as a student in botanical illustration at the State Herbarium of South Australia, prepared the excellent plate of *Grammosolen archeri*. My thanks go to Bill Barker for preparing the distribution map using QGIS and useful GIS layers with point data I provided from the ALA download. My deep gratitude goes to my wife Rosalie Haegi for her support, encouragement and unstinting help throughout the life of the project, not least in assisting with fieldwork.

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Rytidosperma robertsoniae (Poaceae), a new species from southern Australia

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Abstract: It has been known for some years that there is a 2n=24 chromosome race of *Rytidosperma caespitosum* from South Australia. It is unable to hybridize with other forms of the species tested so far and is reliably recognizable by a number of distinct morphological characters. It is here described as a new species, *R. robertsoniae* Tiver, and illustrated. Amendments to *Rytidosperma* keys in the *Flora of Australia* and *Grasses of South Australia* are provided. The type form of *R. caespitosum* from the Shark Bay area, Western Australia, is discussed, described and illustrated; a lectotype is chosen.

Keywords: biodiversity, new species, taxonomy, cytology, Australia, *Rytidosperma*

Introduction

Rytidosperma caespitosum (Gaudich.) Connor & Edgar has long been recognised as "highly variable" (Vickery 1956). Vickery, whilst working on her revision of the then genus *Danthonia* in Australia, was aware that the species exhibited "a wide range of forms", but was frustrated in her attempts to segregate infra-specific taxa, for although certain groups of specimens showed combinations of characters that might justify recognition, other specimens showed recombinations of the characters that "cut across" any projected scheme of classification.

At about the same time as Vickery was working on her revision of the genus, Abele (1959), a cytologist at the Waite Agricultural Research Institute in Adelaide, determined the chromosome number of Australian species of *Danthonia*. Enid Robertson, then curator of the Waite Herbarium, was managing and identifying the *Danthonia* collections for Abele's (1959) project. Abele found three chromosome races within *D. caespitosa*, 2n=24, 48 and 72 (Abele 1959). The majority of material examined was 2n=48; 2n=72 was found in a single population in the Adelaide Hills and a single specimen on southern Eyre Peninsula; 2n=24 was confined to six collections from "drier areas" of South Australia and New South Wales (Table 1). When the Waite Herbarium was closed, Robertson's specimens, notes, unpublished manuscripts and drawings were transferred to the State Herbarium of South Australia (AD). The material had not been disturbed since its transfer to AD, but the specimens had never been assigned herbarium numbers. Of Abele's six n=24 specimens only five were able to be located at AD and one of these, the specimen from Trangie (N.S.W.), I determined to be *R. setaceum* (R. Br.) Connor & Edgar (Table 1, Fig. 1), leaving only four specimens to be examined.

Abele (1959) reported a *pers. comm.* from Enid Robertson that there were a number of distinguishable forms of *D. caespitosa*. Robertson's unpublished manuscripts showed that she recognised 15 forms within *D. caespitosa*, five of which were later identified as other species, leaving ten forms. Her drawing of her Form 6 is clearly consistent with four specimens that Abele determined to be 2n=24. I believe there is sufficient evidence to separate Robertson's Form 6 as a separate species, and refer to it hereafter as *Rytidosperma robertsoniae*.

Shortly thereafter, Brock & Brown (1961) carried out hybridization trials between *Danthonia* species of varying ploidy levels. They obtained much of their material from Robertson's Waite collections (Table 2) and from my examination of the Waite records, it appears that she had supplied seed lines that corresponded with many of her distinct forms (Table 2). Brock and Brown used six seed-lines of 2n=24, including two of the four South Australian *R. robertsoniae* lines, a form from Trangie, and several Canberra lines, which they appear to have collected themselves; these they considered to be functional diploids, 24 being the lowest chromosome number found in the genus in Australia.

Brock & Brown (1961) only gave localities for their material in their Appendix 1, not Waite seed-line numbers, but comparison of their Appendix with the Waite card files of seed lines indicates that at least nine of them were lines that Robertson regarded as typical

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Table 1. Specimens for which Abele (1959) determined the chromosome number as 2n=24. The number in the left-hand column shows the mapped locations of specimens confirmed as Form 6 in Fig. 1. These specimens were collected for agricultural trials at the Waite Institute and do not seem to have been intended to be placed in the herbarium. They are stored in AD vaults, but have not to date been given AD accession numbers: the only identifiers are codes used during Abele's original research project. Collector names, locations and dates were retrieved from Robertson's card-files.

Fig. 1 reference no.	Collector	Location	Region	Date	Robertson form no.
1	C.M. Eardley (Abele 117A)	Koonamore Stn [N Yunta] SA	North-Eastern	28.vi. 1950	6
2	D.E. Symon (Abele 107A)	Terowie Township SA	Northern Lofty	15.vi.1950	6
3	W.C. Johnston (Abele 154A)	Waddikee Rocks [SW Kimba] SA	Eyre Peninsula	2.xi.1950	6
4	A.T. Pugsley (Abele 56)	Arthurton to Ardrossan Road	Yorke Peninsula	23.xi.1950	6
not mapped	R.M. Baker (Abele 114B)	County Jervois	Eyre Peninsula	6.x.1950	specimen not located
not included further	C.W.E. Moore (Abele 110)	Trangie	Central N.S.W.	12.xi.1950	14, *R. setaceum*

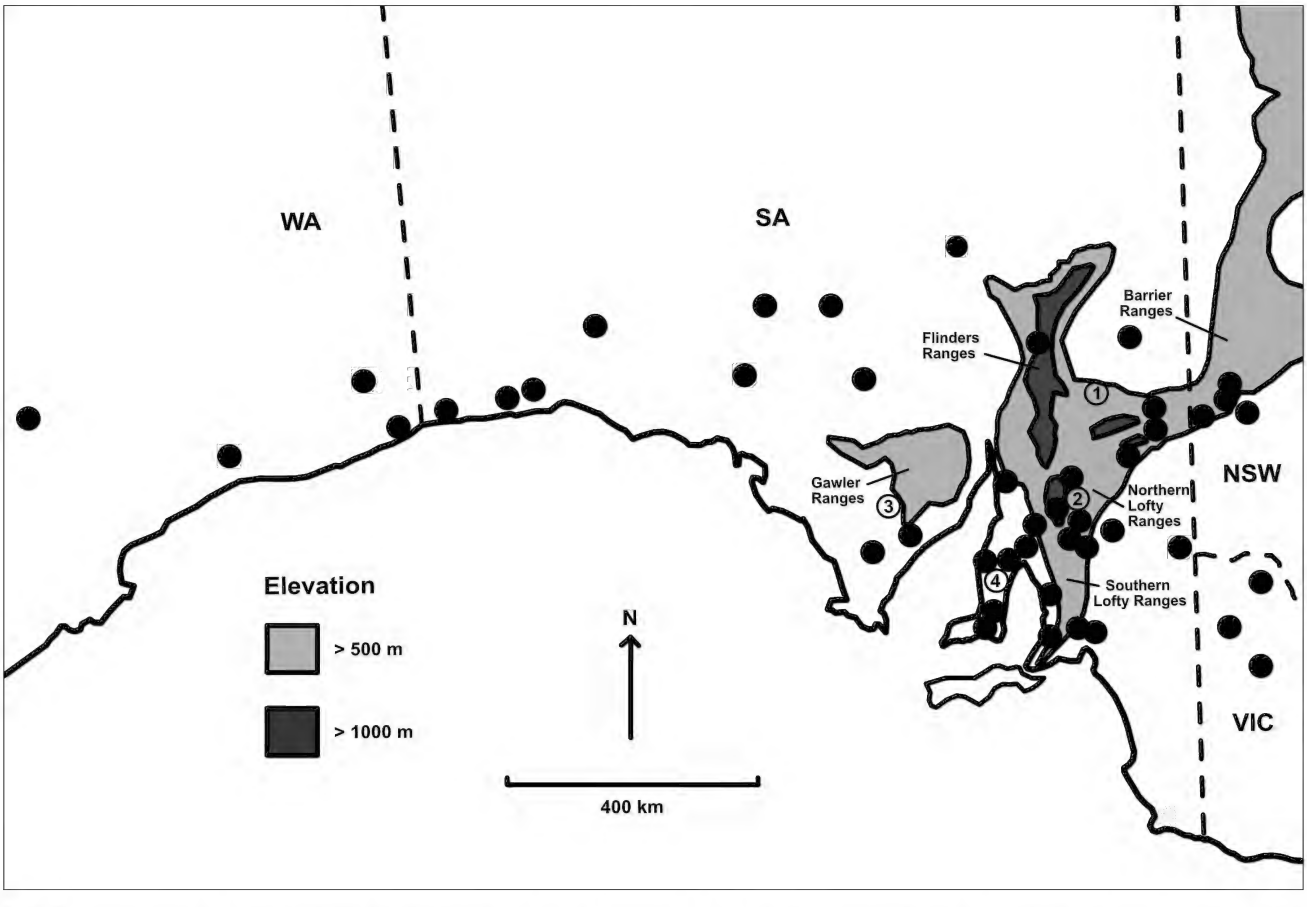

Fig. 1. Distribution of *Rytidosperma robertsoniae* in South Australia (SA), the Nullarbor region of Western Australia (WA), north-western Victoria (VIC) and south-western New South Wales (NSW). Circled numbers mark the locations of the four specimens for which Abele (1959) determined the chromosome count as 2n=24 (Table 1).

of her distinct forms (Table 2), including two of her *R. robertsoniae* lines. Brock and Brown's hybridization trials showed that crosses between any of the six 2n=24 forms (including two lines of *R. robertsoniae*) and any of the 2n=48 or 2n=72 forms produced only lethal hybrids where the seeds either failed to germinate or the offspring died before flowering. They were able to produce viable (though not fertile) offspring when crossing their 2n=24 forms of *R. caespitosum* (including *R. robertsoniae*) with two other species with 2n=24. In retrospect it is unfortunate that Brock and Brown did not distinguish between Robertson's forms and their other 2n forms in their paper, so that when a cross was viable, it is not possible to link that success to any particular form including *R. robertsoniae*, unless their original data can be found.

Table 2. Seed lines of *Rytidosperma* used in hybridization trials by Brock & Brown (1961). Collection details remain unknown for a number of their seed-lines, but they were possibly collected by CSIRO staff.

Brock & Brown location	Waite seed line no.	Collector	Date	Chromosome number (2n)	Robertson form no.
Canberra, A.C.T.				24	
Gilgandra				24	
Cowra				24	
Trangie, N.S.W				24	
Port Augusta	154A	W.C. Johnston	2.xi.1950	24	6
Terowie, S.A.	107A	D.E. Symon	15.vi.1950	24	6
Canberra, A.C.T.	81?	C.W.E. Moore?	14.xii.1950	48	
Coonabarabran				48	
Forbes				48	
West Wyalong				48	
Cowra				48	
Wagga	93?	C.W.E. Moore	15.xi.1950	48	13
Barraba, N.S.W.	103C		9.xi.1949	48	3
Nyah, Vic.	111A	D.E. Symon		48	
Binnum, S.A.	173B	E.L. Robertson	3.xi.1950	48	2
Peterborough, S.A.	26	R.M. Feuerhardt	23.v.1950	48	9
Robe, S.A.	159B?	E.L. Robertson	3.xi.1950	48	4?
Verdun, S.A.	203A	E.L. Robertson	13.xi.1950	48	15
Mt. Lofty, S.A.	202A?	E.L. Robertson		48	10?
Naracoorte, S.A.	176A?	E.L. Robertson	4.xi.1950	48	5
Doodlakine, W.A.	127	J.L. Frith	15.xi.1950	48	12
Clackline, W.A.	125	J.L. Frith	14.xi.1950	48	11
Canberra, A.C.T.				72	
Cowra, N.S.W.				72	
Ambleside, S.A.	205A	E.L. Robertson		72	
Ungarra, S.A.	206B	A.T. Pugsley		72	

Waters *et al.* (2010, 2011) made collections of 343 whole plants from 28 populations of what they considered to be *Rytidosperma caespitosum* over a wide area in central western New South Wales. Due to difficulty in field identification, other *Rytidosperma* species including *R. erianthum* (Lindl.) Connor & Edgar, *R. fulvum* (Vickery) Humphreys & Edgar, *A. bipartitum* (Link) Humphreys & Linder and *R. setaceum* (R.Br.) Connor & Edgar were also included. They grew the plants on under nursery conditions, and used their seed to produce sibling populations, then used both traditional root-squash examination followed by flow-cytometry to determine their ploidy levels. They found that about 20% of *R. caespitosum* plants were diploid (2n=24), about 60% were tetraploid (2n=48), and 9% hexaploid (2n=72); populations included both diploids and tetraploids. They also found occurrences of a rarer intermediate triploid ploidy level (2n=36). Waters *et al.* did not report as to whether there were morphological differences between the ploidy levels. They did not conduct hybridization trials to determine if the 2n=36 plants were able to breed back to the other ploidy levels; however they interpreted the existence of these intermediate triploids as evidence of intra- or inter-specific hybridisation of diploid and tetraploid forms and of polyploid races coexisting within a single stable species.

There are now many more specimens from "drier areas" available for examination. I searched all the collections of *R. caespitosum* in both the Western Australian Herbarium (PERTH) and AD, including all the interstate material held at AD, and discovered that *R. robertsonieae* is actually common and widespread

in dry areas of South Australia, and is reliably distinguished from hundreds of specimens of all the other highly variable forms of *R. caespitosum* observed in both herbaria. Even though Brock & Brown (1961) found that hybrids between species invariably showed intermediate characteristics, *R. robertsoniae* is highly consistent and no obvious intermediates between it and any other forms of *R. caespitosum* were found.

Methods

Dried herbarium specimens were examined from AD and PERTH. A sample of 46 specimens of *R. robertsoniae* representative of different regions of South Australia and all material held from neighbouring states, plus the four Waite specimens (Table 1) was used to derive the description. It is estimated that at least a quarter of specimens in AD currently identified as *R. caespitosum* are actually *R. robertsoniae*.

Data were collected for 87 characters from these 52 specimens of *R. robertsoniae*, some of which were direct measurements, while qualitative characters were assessed on a 1–5 scale. Characters used are shown in the description below. I have used Vickery's (1956) method of measuring the lemma from the sinus to the tip of the callus which is widely followed elsewhere, but it is important to note that Linder's (2005) entry in the *Flora of Australia* does not include the callus in the measurement. Summary statistics of range, minimum and maximum, and standard deviation were calculated in Microsoft Excel. In the descriptions, measurements lie within 2× the standard deviation, and extremes (outside the round brackets) lie beyond 2× the standard deviation.

I visited the Museum of Natural History in Paris (P) and also the Royal Botanic Gardens Kew (K) and examined type material of *Danthonia caespitosum*. There are two specimens in P and one at K. A fourth type-sheet in the Herbarium of the Natural History Museum (BM) was unavailable for examination during my visit to London, but all type specimens are available through JSTOR Global Plants. Measurements from the K and P type specimens were used to identify those specimens in PERTH, which matched the types (see also 'Typification', below).

Taxonomy

Rytidosperma caespitosum (Gaudich.) Connor & Edgar *s.str.*

New Zealand J. Bot. 17: 325 (1979). — *Danthonia caespitosa* Gaudich., *Voy. Uranie* 4: 408 (1826). — *Notodanthonia caespitosa* (Gaudich.) Zotov, *New Zealand J. Bot.* 1: 117 (1963). — *Austrodanthonia caespitosa* (Gaudich.) H.P.Linder, *Telopea* 7(3): 271 (1997). — **Type citation:** "In Novae-Hollandiae orâ occidentali (Baie des Chiens-Marins)". — **Lectotype (here designated):** Baie des Chiens Marins, Nouv. Hollande [Shark Bay, Western Australia, 1819], *C. Gaudichaud s.n.* (P00740227). **Isolectotypes:** P00740226 ex Herb. Drake, K000715697 ex Herb. J. Gay, BM000991548 (photo seen).

Tuft-forming annual or short-lived perennial grass. *Culms* (8–) 20–50 (–60) cm long, (0.25–) 0.7–1.5 (–2) mm broad, almost smooth to faintly ribbed, without purple flecks, glabrous or very sparsely microscaberulous. *Nodes* purple (brownish if dried when immature), rather waxy. *Basal leaves* 14–30 cm, wavy, glabrous or very sparsely microscaberulous, occasionally with scattered longer hairs 0.1–0.5 mm long, tubercles usually not enlarged, or enlarged and 0.5–0.1 mm broad. *Culm leaves* 2.5–10 cm long, loosely or tightly rolled, 0.5–2 mm broad, upper surfaces moderately to densely hairy, the hairs 0.1–0.5 mm long, densely waxy. *Collar hairs* (2.5–) 3–4 mm. *Ligule hairs* 0.75–1.5 mm. *Sheaths* moderately ribbed above, unpigmented or lightly dotted purple, glabrous or microscaberulous, moderately waxy. *Panicle* not or shortly exserted from the uppermost sheath by 0–3 cm, 3–8.5 cm long, 1.5–2.5 cm broad, lanceolate, oblong or ovate in outline, with 10–30 (–36) spikelets, branches sparsely to moderately pubescent with hairs 0.2–0.6 mm long, green-straw or slightly flecked purple. *Pedicels* 3–4 mm long, straight or slightly curved, moderately pubescent with hairs 0.1–0.3 mm long, green-straw or flecked purple. *Spikelets* 11–17 mm long, with 5 or 6 florets, awns enclosed or exceeding the glumes by up to 3.5 mm. *Lower glume* 11–16 mm long, 2.5–3.5 mm broad, with 5–7 nerves, broad-lanceolate, green-straw or slightly flecked purple above, near glabrous or very sparse microscaberulous above, distinctly narrowed above, with scarious tips 0.5–4.5 mm long, keels scaberulous above, margins 0.75–0.9 mm broad, unpigmented or slightly to moderately streaked purple. *Lemma* 3–4 mm long including callus, 1.3–2.4 mm across the flattened sinus, moderately thick and firm, rounded in cross-section, slightly to moderately convex from sinus to callus, golden-straw when dry, moderately shining, ribs faint to obscure, glabrous on the backs between the rows of tufts, or with a few sparse fine hairs 0.3–0.75 mm long. *Callus* 0.5–0.9 mm long. *Callus hairs* 0.9–1.2 mm long, overlapping the lower row of tufts on the lemma by 0.1–0.2 mm. *Upper row of tufts* of the lemma set 0.6–0.8 mm below the sinus, hairs 3–4.75 mm long, sparse to moderately dense, overlapping the flat lobes by 0.7–1.1 times. *Lower row of tufts* with hairs 1.5–2 mm long, not or well-overlapping the upper row by (-0.3–) -0.2–0.75 mm, rather sparse, the central and sometimes the second pair of tufts next to the midrib often shorter, sparser or entirely absent. *Lobes including setae* 4–7 mm long, 1.2–1.8 times the lemma, flat lobes 1.7–3.25 mm long, 0.75–1.3 times the lemma, moderately ribbed. *Lobe wings* 0.2–0.3 mm broad, usually about the same width as the fleshy lobe or slightly narrower or broader, merging acutely or more gradually into the setae, unpigmented or occasionally lightly to moderately streaked purple. *Setae* 1.5–2.5 mm long, occupying 0.3–0.45 the total lobes, unpigmented or purple. *Central awn shaft* 3.5–8 mm long, exceeding the setae

by 2–7 mm, blotched purple in the middle, sometimes unpigmented. *Column* 2.5–5 mm long, 0.2–0.3 mm broad at the base, not, just reaching or exceeding the flat lobes by (-0.5) 0–0.9 (–1.5) mm, twisted (1–) 2–3 (–4) times, golden-brown to copper-brown. *Palea* 3.25–4 mm long, 0.75–1 mm broad, exceeding the sinus by 0.75–1.2 mm, lanceolate or narrow-ovate, ciliolate on the upper third to half of the margins, keel-hairs sparse to moderately dense, 0.5–1.5 mm long, glabrous on the backs between the keels, the backs moderately shining, not to very slightly narrowed but transparent above for 0.6–1.8 mm, shortly notched at the tip (0.01–) 0.03 (–0.05) of the palea, the transparent part 0.1–0.3 (–0.4) of the total length of the palea measured to the tip of the cleft. *Anthers* c. 0.6 mm long, pale yellow. *Caryopsis* 1.6–1.8 mm long, 0.6–0.8 mm broad, obovate, honey-brown to red-brown, faintly warty on the outer surface, embryonic axis linear to narrow-oval, scutellum narrow-oval to oval.

Typification. Gaudichaud cites one gathering of *D. caespitosa* from Shark Bay in the protologue. Vickery

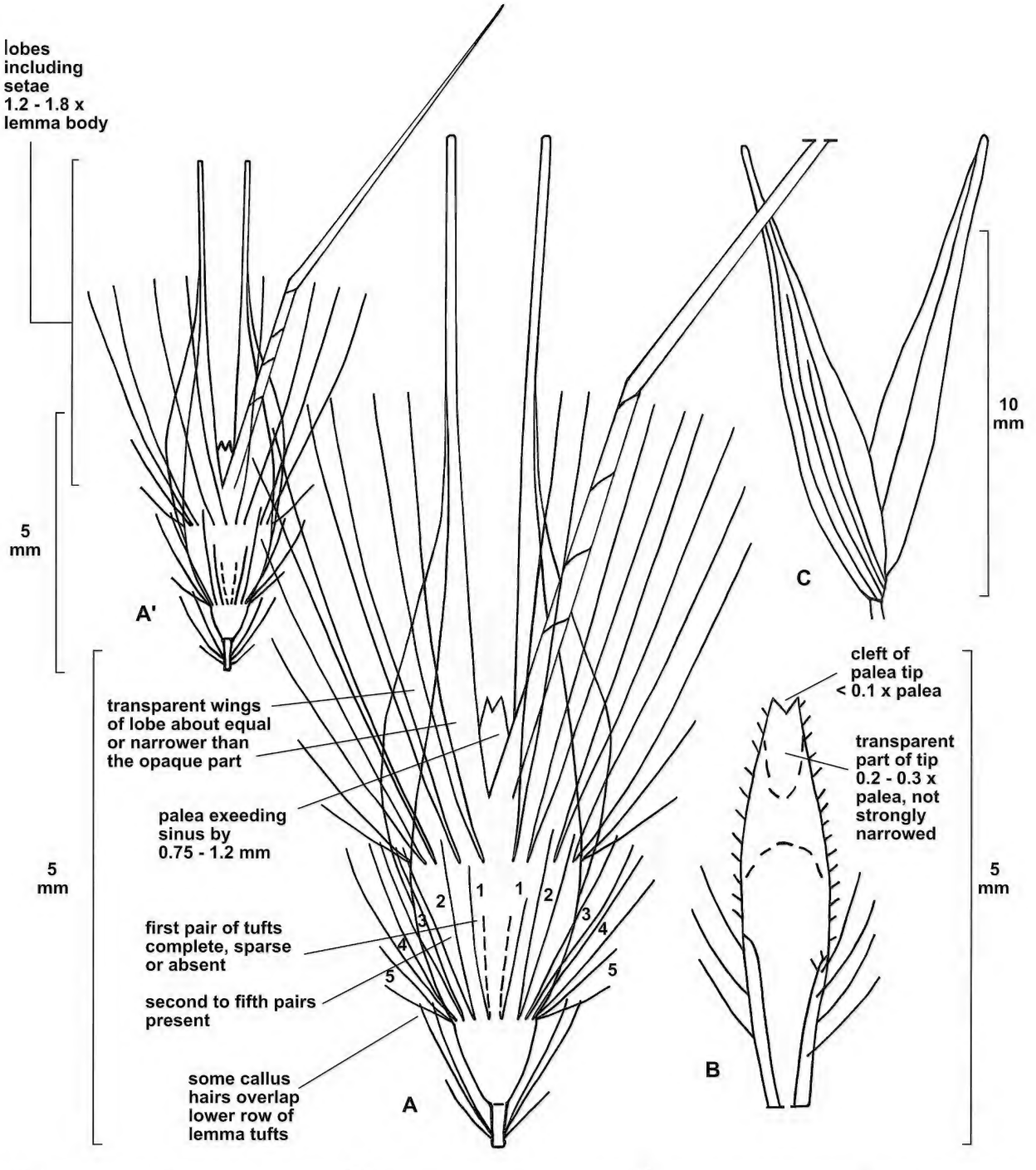
lobes including setae 1.2 - 1.8 x lemma body
5 mm
A'
transparent wings of lobe about equal or narrower than the opaque part
palea exeeding sinus by 0.75 - 1.2 mm
5 mm
first pair of tufts complete, sparse or absent
second to fifth pairs present
some callus hairs overlap lower row of lemma tufts
A
1
2
3
4
5
C
10 mm
cleft of palea tip < 0.1 x palea
transparent part of tip 0.2 - 0.3 x palea, not strongly narrowed
B
5 mm

Fig. 2. *Rytidosperma caespitosum* lectotype. **A** Lemma, central awn truncated; **A'** lemma at lower magnification with complete central awn; **B** palea; **C** glumes. Five pairs of hair-tufts of the lower row on the lemma back numbered 1 (central) to 5 (lateral), only the outer hairs of each tuft depicted for clarity. — Illustration by the author from: *C. Gaudichaud*, Baie des Chiens Marins Nouv. Hollande [Shark Bay, Western Australia], 1819 (P00740227).

(1956) lists the "holotype" to be located in P, but does not mention other herbaria. However, there are actually two specimens at P and one each in K and BM (first mentioned by Linder 1997); all four specimens are very similar and apparently from the same gathering. In Vickery's other descriptions of *Rytidosperma* species (1956), she only ever cites a single specimen as the "holotype", with any other type material listed as "duplicates". It seems likely that there was only one specimen available in P to Vickery at the time.

P00740227 is annotated by Gaudichaud, has complete culms with roots still attached and is labelled "syntype". P00740226 from the herbarium of Emanual Drake del Castillo, consists only of two panicles, and is likewise labelled "syntype". K000715697 has three culm fragments and two panicles and is labelled "holotype"; it is from herbarium of Jacques Étienne Gay and marked "Gaudichaud dedid Xbr 1825", i.e. it was given to Gay by Gaudichaud in that year. BM000991548 has a tuft of fertile culms with some roots attached, plus a separate culm with panicle; it is annotated "recd [received] 1825 from M. Gaudichaud".

While Art. 9.10 (Turland *et al.* 2018) states that the use of the term "holotype" by Vickery (1956) can be corrected to "lectotype", it is unclear which of the two specimens at P she actually examined. There are no notes or det-slips by Vickery attached to the specimens. As such, it is necessary to designate a lectotype: I chose P00740227 as the best available specimen, with the other collections being isolectotypes.

Note. The only PERTH specimens matching the type collection of *D. caespitosa* are restricted to the Shark Bay area. The type form is distinguished from all other material of *R. caespitosum* that I have examined so far in PERTH and AD by having only shortly elongated lobes including setae, only 1.3–1.8 times the lemma, the only consistent difference, but a very important one in a genus where the relative lengths of parts are often diagnostic. In all other forms of *R. caespitosum* examined, the lobes including setae are at least twice the length of the lemma.

Gaudichaud's original Latin description is, as was then commonly accepted, very brief, and, in the years since, published descriptions of *R. caespitosum* have been much expanded by other authors over the years, in an attempt to encompass the high level of variation in what is currently recognised as *R. caespitosum*. I considered it useful to provide a description of *R. caespitosum s.str.*, based on my measurements of P00740227 and eight other specimens from the Shark Bay region in PERTH. The description and illustration will be indispensable should any further segregation of taxa from *R. caespitosum* be carried out in the future.

It is even more important to have a detailed drawing (Fig. 2) and description of the lectotype, because all three type specimens I have seen are suffering from an identical form of gelatinous deterioration, presumably relating to their being subject to some form of contamination. That they are all suffering the same deterioration tends to confirm that the four specimens are duplicates, with the contamination occurring before the original collection was divided.

Other specimens examined

WESTERN AUSTRALIA: *J.J. Alford & M. Trudgen 1369*, Three Bays Island, Shark Bay, 14.ix.1989 (PERTH01451685A); *J.J. Alford & M. Trudgen 1271*, Salutation Island, Shark Bay, 12.ix.1989 (PERTH01451162); *T.E.H. Aplin 3475*, Heirisson Prong [Cape Harrison], Shark Bay, 13.viii.1970 (PERTH00293199); *A. Markey 1825*, Edelland, Shark Bay, 18.ix.1997 (PERTH05252415); *A. Markey 1716*, Steep Point, Shark Bay, 20.ix.1997 (PERTH05249295); *A. Markey 1736*, ~12 km S-SSW Useless Loop Town & Trig, Shark Bay, 28.ix.1997 (PERTH05249120); *A.S. George s.n.*, East Fisherman Paddock, Dirk Hartog Island, Shark Bay, 4.ix.1972 (PERTH00293121A); *P. Morat 8338*, False Entrance, Shark Bay, 24.vii.1988 (PERTH01780514).

Rytidosperma robertsoniae Tiver, *sp. nov.*

Holotypus: SW Kimba, Eyre Peninsula Region, South Australia, 15 Oct. 1953, *J.G.[B.] Cleland s.n.* (AD97222040). **Isotypi:** CANB, MEL, NSW, PERTH, K. — This collection is the basis of seed-line ELR 154A, used by Abele (1959) and Brock & Brown (1961), i.e. the chromosome number is known to be 2n=24.

Danthonia caespitosa Form 6: E.L.Robertson in K.Abele, *Trans. Roy. Soc. S. Austral.* 82: 163–173 (1959). 24-chromosome race.

Danthonia caespitosa 2n=24: R.D.Brock & J.A.M.Br., *Austral. J. Bot.* 9(1): 62–91 (1961).

Danthonia caespitosa auct. non Gaudich: A.P.C.Renfrey in Jessop & Toelken, *Fl. S. Austral.* 4: 1858 (1986), partly.

Nothodanthonnia caespitosa auct. non (Gaudich.) Zotov: Zotov, *New Zealand J. Bot.* 1: 117 (1963), partly; H.P.Linder & Verboom, *Telopea* 6(4): 615 (1996), partly.

Austrodanthonia caespitosa auct. non (Gaudich.) H.P.Linder: H.P.Linder, *Telopea* 7: 271 (1997), partly; H.P.Linder in K.Mallett, *Fl. Austral.* 44B: 53 (2005), partly; Jessop *et al.*, *Grasses S. Austral.* 287 (2006), partly.

Rytidosperma caespitosum auct. non (Gaudich.) Connor & Edgar: Connor & Edgar, *New Zealand J. Bot.* 17: 325 (1979), partly.

Tuft-forming annual or short-lived perennial grass. *Culms* short to medium height, occasionally dwarfed, rarely tall, (11–) 18–32 (–44) cm long, (0.5–) 0.6–1 (–1.4) mm broad (measured shortly below node to avoid destroying sheaths to obtain lower measurements), slightly ribbed, flecked purple especially near nodes, glabrous or sparsely scabrid. *Nodes* purple to dark-purple. *Basal leaves* (1–) 5–16 (–26) cm long (sheath and blade), strongly sinuate to falcate, unpigmented or slightly streaked purple near tips, with sparse to moderately dense hairs, (0–) 0.25–1.9 (–2.5) mm

long, hairs usually with enlarged tubercle-bases, 0.05–0.2 mm broad, occasionally glabrous. *Culm leaves* (1–) 2.5–8.5 (–13) cm long, tightly rolled when dry, (0.3–) 0.4–0.9 (–1.3) mm broad, upper surfaces moderately to densely pubescent with hairs (0–) 0.1–0.7 (–1.5) mm long. *Collar hairs* (1.25–) 2–3.5 (–5) mm long. *Ligule* a fringe of hairs, longest hairs (0.5–) 0.6–1.1 (–1.5) mm. *Sheaths* sparsely scabrid or occasionally with hairs, 0.1–2.5 mm long, on enlarged tubercles, 0.05–0.1 mm broad, moderately ribbed above, unpigmented or lightly streaked purple. *Panicle* not or shortly exserted from sheath at seed maturity by 0–5.5 (–13) cm, panicle (3–) 4–7 (–8.5) cm long, (1.5–) 2–3.5 (–4) cm broad, ovate, oblong or broad-lanceolate in outline, with (5–) 7–17 (–35) spikelets, branches sparsely to moderately pubescent with hairs 0.1–0.5 mm long, unpigmented or slightly to moderately streaked purple. *Pedicels* (3.5–) 4.5–7.5 (–10) mm long, straight or slightly curved, pubescent with hairs 0.1–0.75 mm long, with longer hairs above to 1.2 mm long, slightly to quite densely streaked purple. *Spikelet* (14.5–) 19.5–25 (–28) mm long including setae, with (5–) 6–8 (–9) florets, setae exceeding glumes in spikelet by 1–6 (–8) mm. *Lower glume* with (3–) 4–6 (–9) veins, (14–) 16–21 (–25.5) mm long, 3–4 (–5) mm broad, broadly lanceolate, moderately to abruptly narrowed above, with scarious tips (0–) 1.5–4.5 (–8) mm long, glume-body yellowish often slightly purple-streaked, glabrous or sparsely scabrid, keels sparsely tuberculate or shortly scabrid in upper third. *Membranous glume-margins* 0.7–2 mm broad, streaked purple half or full length of margin, occasionally unpigmented. *Upper glume* lanceolate or more often broad-lanceolate, opaque bodies nearly always flecked or streaked purple, slightly to abruptly narrowed above, upper glume margins 1–1.4 mm broad, frequently streaked or blotched purple, very rarely unpigmented. *Lemma* (3–) 2.5–4.5 (–5) mm long from sinus to tip of callus, c. 2 mm broad at sinus, narrow-oblong to narrow-triangular, broadest point across sinus, well-rounded to somewhat compressed in cross-section, moderately to strongly indurated, yellowish to golden, shining, mid-rib of lemma faint to slightly raised, lateral ribs obscure to faint, surface between the two rows of hair-tufts always completely glabrous. *Hairs of upper row of tufts* (below sinus) set (0.4–) 0.5–0.7 (–0.9) mm below sinus, (3–) 4–5.3 (–6) mm long, partially overlapping by (0.35–) 0.5–0.7 (–0.9) flat part of lemma lobes, hair-tufts complete (all 8 dorsal tufts present), moderately to very dense with many hairs, but often with quite a few shorter hairs. *Tufts of lower row of hairs* (above callus) interrupted, first pair of tufts next to midrib totally absent or rarely reduced to a few very short bristles, second pair of tufts moderately to very densely hairy and raised on distinct ledge-like protuberances of the lemma back, third pair complete, reduced and set higher than the other tufts, or absent, fourth pair moderately to very dense and raised on distinct protuberances, hairs of the four dense tufts, (1–) 1.6–2.5 (–3) mm long, most of the hairs very short and not reaching, or some hairs just reaching, or slightly overlapping upper row of tufts. *Callus* (0.5–) 0.6–1 (–1.25) mm long, with hair-tufts (0.5–) 0.7–1.2 (–1.6) mm long, hair-tufts barely as long as callus and never reaching row of tufts above callus, falling short of it by (0.15–) 0.22–0.45 (–0.6) mm. *Lateral lemma lobes* (including setae) (7–) 9–13 (–14.5) mm long, (1.8–) 2.3–3 (–3.9) times as long as lemma, flat part of lobes (1.1–) 1.3–1.7 (–1.9) times as long as lemma, moderately to prominently ribbed, unpigmented or somewhat flecked purple above. *Setae* (2.5–) 3.5–6 (–8.5) mm long, occupying (0.25–) 0.4–0.5 (–0.6) the length of the total lobes, moderately flecked to dark purple. *Membranous (nerveless) lobe wings* (0.2–) 0.4–0.6 (–0.75) mm broad at their widest point and usually slightly broader or much broader than the opaque (innervated) part of the lobe, narrowing acutely to rather abruptly into the setae, commonly streaked purple, occasionally unpigmented. *Central awn & column* (12.75–) 15–20.5 (–26) mm long. *Awn shaft* (8.5–) 10–14 (–18) mm long, streaked purple for at least half its length, rarely unpigmented, exceeding setae by (4.8–) 6–9 (–14) mm. *Awn column* (4.25–) 5–6.5 (–8) mm long, either shorter by up to 3 mm or longer by up to 3 mm than the flat part of the lobes, (0.2–) 0.3–0.4 mm wide across its base at the sinus, twisted (2–) 2.5–4 times, golden-brown to dark-brown at maturity. *Palea* narrow-lanceolate or narrow-elliptic, (4–) 4.5–5.8 (–6.5) mm long, (0.75–) 0.9–1.1 (–1.35) mm broad at the widest point which is (0.3–) 0.4–0.6 (–0.7) of the total length, exceeding sinus by (0.75–) 1.5–2.4 (–2.9) mm, reaching up to (0.1–) 0.25–0.4 (–0.55) of the flat lobes, the tip deeply cleft, the teeth (0.3–) 0.04–0.07 (–0.8) of the palea, distinctly narrowed above the caryopsis into a long transparent tip (0.25–) 0.3–0.5 (–0.6) of the length, keel-hairs sparse to moderately dense, (1–) 1.2–1.8 (–2.5) mm long, surface between keels glabrous and highly shining, apex bifid with cleft 0.2–0.35 (–0.6) mm deep. *Anthers* (1.2–) 1.5–2.3 (–2.5) mm long, commonly pale to dark-purple, occasionally pale gold (possibly when immature). *Caryopsis* obovate, (0.4–) 0.6–1 (–2.3) mm long, (0.4–) 0.6–1 (–1.2) mm broad, honey to red-brown, faintly warty on adaxial surface, embryonic axis narrow-oval, scutellum narrow-oval to oval.

Distribution and Habitat. Abele (1959) suggested that *R. robertsoniae* is most common in drier environments, and the distribution of the specimens examined supports his comment (Fig. 1). This statement is also supported by the observations of Waters *et al.* (2010) in New South Wales, where diploids were associated with a lower mean annual rainfall for a number of *Danthonia* species. It is currently recognised from across the drier regions of southern Western Australia and South Australia and from Broken Hill in New South Wales to north-western Victoria. It is notably absent from the higher rainfall regions and more mesic habitats of the South Australian ranges. The area that *R. robertsoniae* inhabits is associated with Oligo-Miocene marine incursions of the Eucla and Murray basins (Quigley *et al.* 2010). The Eucla Basin once covered the area we now know as the Nullarbor Plain, and also coastal regions of Eyre Peninsula, all of Yorke Peninsula, and

the Adelaide plains. The Murray Basin abutted the eastern side of the Flinders Ranges, and extended into south-west New South Wales and north-west Victoria. The soils of these regions are, being of marine origin, solonized (saline) calcarosols (limestone) and alkaline (Isbell 2002). The specimens listed below for *R. robertsoniae*, where ecological information is given, were found on solonized heavy clays, clays,

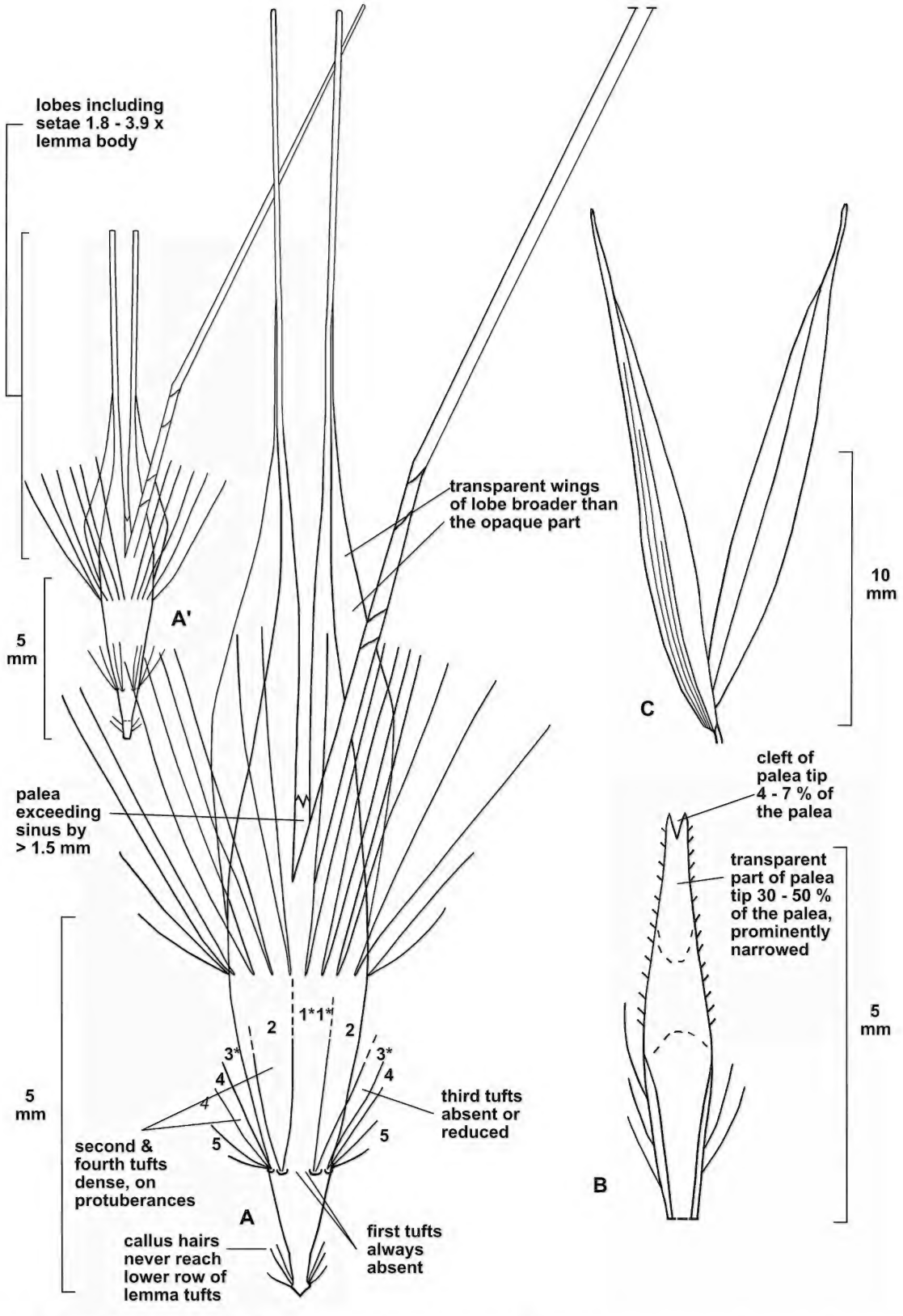

Fig. 3. ***Rytidosperma robertsoniae*.** **A** lemma, central awn truncated; **A'** lemma at lower magnification with complete central awn; **B** palea; **C** glumes. Locations of five pairs of hair-tufts of the lower row on the lemma back numbered 1 (central) to 5 (lateral), only the outer hairs of each tuft depicted for clarity. Absent tufts indicated by asterisks. — Illustration by the author from: *W.C. Johnston*, Waddikee Rocks, 2.xi.1950 (AD).

and calcareous sandy loams of inland plains, inland limestone ridges and outcrops, in limestone crevices of coastal cliffs, and in one case on a gypsum dune (*D.E. Symon & J. Symon 16660*). That *R. robertsoniae* can thrive in these harsh soils and climates indicates a tolerance to high levels of aridity, alkalinity and salinity not found in most other species of *Rytidosperma*. This level of ecological specialization is further evidence of the likelihood that *R. robertsoniae* is a separate species from other forms of *R. caespitosum*. It is likely that *R. robertsoniae* is more common in neighbouring states than these results, mostly based on South Australian herbarium material, indicate.

Phenology. Specimens with mature spikelets have most often been collected between August and December, peaking in September, indicating that the species derives from sites showing a typical winter rainfall pattern. However, fertile specimens have been collected in April and June, suggesting that *R. robertsoniae* can take advantage of seasonal conditions, and may behave as a short-lived perennial if conditions allow.

Conservation Status. *Rytidosperma robertsoniae* appears to be common and widespread, and its conservation is probably not at any immediate risk. However, land clearance, especially in the southern part of its range, would have resulted in fragmentation of its population. If land rehabilitation is carried out in these areas, it would be useful to be able to identify if *R. robertsoniae* was originally the dominant form, because re-seeding with other species or forms of *Rytidosperma* may not be successful in alkaline, saline soils inhabited by *R. robertsoniae*.

Etymology. The specific epithet is in honour of Mrs Enid Robertson who, as systematic botanist at the Herbarium of the Waite Agricultural Institute in the 1950s, first recognised *R. robertsoniae* as a distinct form.

Distinguishing characteristics of **Rytidosperma robertsoniae.** The description of *R. robertsoniae* is based on the four specimens of Robertson's Form 6 and 46 other specimens. They were consistent in the following characters, in which they are distinguished from *R. caespitosum s. str.* and all other forms seen of *R. caespitosum*.

(1) **Reduction in number of hair-tufts of the lower row of the lemma and raising of the remaining tufts on protuberances.** One of the Abele specimens of *R. robertsoniae* is illustrated in Fig. 3. The specimen confirms what Abele (1959) recorded in his drawing: this 24-chromosome plant has a reduced number of hair-tufts in the lower row of the two rows of hairs across the backs of the lemma commonly seen in *R. caespitosum*. A *Rytidosperma* lemma has nine nerves and, even if the nerves themselves are obscure because of thickening of the lemma, they govern where the tufts occur, i.e. between the ribs; in a specimen with a complete row of tufts, there are eight dorsal tufts plus two lateral tufts, i.e. 5 pairs of tufts on each side of the mid-rib (central nerve) (Fig. 2). In *R. robertsoniae* the first pair of tufts, next to the midrib, is absent and the second pair, out from the midrib, is very dense and each tuft is raised on a distinct protuberance (Fig. 3). The third pair may be complete, sparse or absent. The overall appearance is distinctive, of apparently four or six very dense tufts, with a gap where the two central tufts are absent, and sometimes two other gaps where the third tufts are absent. When both the central and third tufts are absent, the remaining tufts are often very short, giving a very distinctive appearance. Very occasionally, the central pair of tufts are not entirely absent, with one or both of the tufts replaced by a few very short bristles.

Taken by itself, a reduced number of hair-tufts in the lower row of tufts of the lemma is not always diagnostic in separating *R. robertsoniae* from the rest of the widespread and variable *R. caespitosum*; the lectotype of *R. caespitosum* also has two very sparse, nearly absent, central tufts (Fig. 2) and I have noticed other specimens of *R. caespitosum s.lat.* where the tufts are sparse or nearly absent in both the lower and (less frequently) the upper row. However, in *R. robertsoniae*, the combination of one or two pairs of tufts being absent with the remaining tufts being very dense and raised prominently on protuberances (see below) is diagnostic.

(2) **Hair-tufts of the callus.** Another diagnostic feature of *R. robertsoniae* relates to the pair of hair-tufts arising from the callus. In all other forms of *R. caespitosum* seen, including the type material (Fig. 2), at least some of the callus hairs are long enough to overlap the lower row of hair-tufts on the lemma-back; however, in *R. robertsoniae*, the callus hairs are very short, often not reaching the junction of the lemma and callus, and never reaching the base of the lower row of hair-tufts on the lemma-backs (Fig. 3A).

(3) **Palea.** In *R. robertsoniae* the palea long exceeds the sinus of the lemma (where the two lateral lobes meet), usually by at least 1.5 mm (Fig. 3). This in itself is not diagnostic as some other forms of *R. caespitosum s.lat.*, have paleas long-exceeding the sinus, though the type form has the palea only shortly or moderately exceeding the sinus by 0.75–1.2 mm. Diagnostically, comparative to the type form of *R. caespitosum*, the upper part of the palea, above where the caryopsis sits, is narrowed and drawn out into a long transparent tip, occupying (0.25–) 0.3–0.5 (–0.6) of the length of the palea, measured to the tips of the cleft. The tip of the palea is also more deeply cleft than other forms of *R. caespitosum*, (0.03–) 0.04–0.07 (–0.08) of the palea. In *R. caespitosum s.str.* the cleft at the tip of the palea is shallow, about 0.03 of the palea, and the transparent part is short or of moderate length, 0.2–0.3 (–0.4) times the length of the palea.

(4) **Lobe wings.** The membranous lobe wings of the lateral lobes of the lemma are very broad in *R. robertsonieae* (Fig. 3). The lectotype of *R. caespitosum* (Fig. 2), and most other forms of *R. caespitosum*, have lobe wings that are usually about equal to or narrower than the width of the opaque part of the lobe, whereas in *R. robertsoniae*, the lobe wings are usually noticeably broader than the opaque part of the lobe at their widest point. The broad lobe wings of *R. robertsoniae* have occasionally led to mis-identifications as *R. laeve* (Vickery) Connor & Edgar, which also has broad lobe wings, but is distinguished by a much broader palea.

(5) **Length of Lobes.** In *R. robertsoniae* the lateral lobes, including the lateral awns (setae), are elongated, 1.8–3.9 times the length of the lemma body. There is a wide range of elongation of the lateral lobes in *R. caespitosum s.lat.*, even approaching the extreme elongation seen in *R. setaceum*. However the type form of *R. caespitosum* is distinctive in having comparatively short lateral lobes, 1.2–1.8 times the length of the lemma body. In this regard, *R. caespitosum s.str.* approaches the appearance of *R. tenuius*, but has a narrower palea and lacks the hairiness of the palea between the keels.

(6) **Cytology.** *Rytidosperma robertsoniae* has the chromosome number, 2n=24, whilst the majority of other specimens of *R. caespitosum s.lat.* are 2n=48, with occasional 2n=72 (Abele 1959). *Rytidosperma robertsoniae* is one of a number of species in the genus with chromosome number 2n=24, and it has been shown to be capable of producing viable offspring when crossed with *R. racemosum* and *R. auriculatum* (Brock & Brown 1961). It is therefore possible that *R. robertsoniae* is a parent of one or more of the many forms of *R. caespitosum* with 2n=24. Molecular work might be able to establish if this is the case.

Other specimens examined (in addition to the specimens listed in Table 1)

WESTERN AUSTRALIA. **Nullarbor:** *T.E.H. Aplin & M. Trudgen 5742*, Railway, 175.5 miles [282 km] E Kalgoorlie, vi.1974 (PERTH00284998); *A.C. Beauglehole ACB 49417*, 19 km W Eucla, 30.viii.1974 (PERTH00294667); *R. Davis 9229*, 37 km NW Cocklebiddy, 5.vi.2000 (PERTH 05921651); *A.S. George 8490*, 20 miles [32 km] SW Reid, 14.x.1966 (PERTH00295108).

SOUTH AUSTRALIA. **Lake Eyre:** *R.J. Bates 35142*, Mount Hamilton, 6.xi.1993 (AD99426238). **Nullarbor:** *R.J. Chinnock 1188*, Eyre Highway, 15 km E Koonalda, 20.ix.1973 (AD97346388); *A. Robinson NPNU-7503*, 21 km NW Nullarbor Station, 21.ix.1984 (AD98526024); *H.R. Toelken 7757*, Highway, 42.7 km W Nullarbor, 29.ix.1987 (AD98747090); *D.J.E. Whibley 4510*, Eyre Highway, 40 km E SA-WA Border, 27.x.1974 (AD97506131). **Gairdner-Torrens:** *R.J. Bates 32019*, Garden Well Island [Lake Gairdner], 10.iv.1993 (AD99336340); *R.J. Bates 50031*, Hill off Tarcoola Road, 14.iv.1998 (AD100872); *H. Vonow & N. Neagle GS721-241*, Bon-Bon to Mt Eba Road, 26.x.2010 (AD241644). **Flinders Ranges.** *R.J. Bates 22926*, Dawson Range [N Peterborough], 13.iv.1990 (AD99026113); *S.T. Blake 16901*, Near Blinman, 31.viii.1946 (AD96942419); *J.B. Cleland s.n.*, ~10 km E Port Germein, 15.ix.1942 (AD96228264). **Eastern:** *R.J. Bates 41213*, near Olary, 2.x.1995 (AD99744081); *J.B. Cleland s.n.*, Oakbank Station [E Burra], 12.ix.1968 (AD96903005); *R.L. Crocker s.n.*, Poalka Paddock, Bimbowrie Station [NE Yunta], 23.ix.1939 (AD98591949); *T.G.B. Osborn s.n.*, Mt Victor Paddock, Koonamore Station, 12.xii.1924 (AD97741269); *SA Pastoral Board s.n.*, Dlorah Downs Station [E Yunta], 1.xi.1956 (AD97916002). **Eyre Peninsula:** *K. Alcock 2429*, Hundred of Rudall, Hincks National Park, 13.xi.1968 (AD96922395); *F.J. Badman 4549*, Carriewerloo Bluff, 23.ix.1990 (AD99052153); *K.L.Graham, H. Stewart & N. Cotsell BS131-461*, Hincks Conservation Park, 8.2 km ESE Tooligie, 2.xi.2001 (AD129102); *L. Heard & G. Carpenter BS131-203*, Hincks Conservation Park, 9 km SSE Tooligie, 3.xi.2001 (AD128694). **Northern Lofty:** *R.J. Bates s.n.*, Bundaleer Forest, 1.xi.1983 (AD99427041); *D. Murfet & L. Heard BS49-375*, Swampy Flat Road, Hanson, 22.x.1992 (AD99532585); *N.M. Smith 2763*, 26 km E Lochiel, 4.viii.1991 (AD99145143); *J.Turner & A.Brown BS162-3348*, 5.2 km WNW Yacka, 3.xi.2004 (AD186513). **Murray:** *J. Carrick 3679*, Near Mallee View Homestead, Monarto, 30.ix.1974 (AD97443119); *J.B. Cleland s.n.*, Chauncy's Line [SW Callington], 12.x.1938 (AD96228258); *D.D. Cunningham, H. Vonow & R. Ferguson 1373*, Hopkins Creek [SW Burra Gorge], 11.xi.2003 (AD161478); *E.H. Ising s.n.*, Koomooloo Stn [NE Burra], 24.ix.1937 (AD97805248); *L.A. Malcolm & K.L. Graham BS62-2537*, 11.3 km NNE Mount Bryan East, 24.x.1994 (AD99717263). **Yorke Peninsula:** *D.A. Cooke 613, Curramulka to Ardrossan Road*, 28.x.1991 (AD99152117); *H. Short s.n.*, Port Moorowie, 17.xi.2010 (AD244610); *D.E. Symon s.n.*, Near Norris Property, Paskeville, 8.x.1952 (AD98591821); *D.E. Symon & J. Symon 16660*, Lake Fowler [N Moorowie], 7.xi.2001 (AD123389); *D.J.E. Whibley 8194*, Dowling Drive, Port Hughes, 9.ix.1982 (AD98238428). **Southern Lofty:** *J.B. Cleland s.n.*, Pedlar's Creek, Noarlunga, 15.x.1927 (AD96228291); *J.B. Cleland s.n.*, Marino Cliffs, 8.x.1932 (AD96225149); *D.J.E. Whibley 8753*, Aldinga Bay, 3.ix.1983 (AD98402260); *Anon. s.n.*, Roseworthy Agricultural College, xii.1931 (AD966072511).

NEW SOUTH WALES. **Western:** *E.C. Andrews s.n.*, Broken Hill, ix.1918 (AD98529272); *P.L. Milthorpe 512*, Ophara [SW Broken Hill], 1.ix.1971 (AD97242126); *E.R. Reed 9*, Vicinity of Broken Hill, 1921 (AD97327076); *L. Richley 1128*, Menindee Road from Broken Hill, 5.ix.1973 (AD97405170).

VICTORIA. **North-West:** *M.D. Crisp 3293*, 30 km SSW Mildura, 9.x.1977 (AD97834068); *M.G. Corrick & P.S. Short 6605*, 5 km SW Sunset Tank, 28.ix.1980 (AD98051013); *A.C. Beauglehole & E.W.Finck 29307*, Wyperfield National Park, 1.ix.1973 (AD98015019).

Discussion

There are now a great many more, and a better geographic spread, of specimens of *R. caespitosum* available in herbaria than were available to Vickery (1956), Robertson (unpubl.), Abele (1959) and Brock & Brown (1961). Vickery (1956) seems to have examined all the specimens available in Australian herbaria at that time,

Alterations required to published keys to distinguish *Rytidosperma robertsoniae*

Additional couplets required are marked with the suffix 'a'.

The entry for *Rytidosperma* (syn. *Austrodanthonia*) in the *Flora of Australia* (Linder 2005) becomes:

27: Glumes only slightly longer than florets, 3.5–4 mm wide **27a**

27a. Hair-tufts of the lower row next to the central rib absent, remaining tufts very dense, raised on distinct protuberances . . . . . ***R. robertsoniae***

27a: Hair-tufts of the lower row complete or, if absent, then remaining tufts not very dense nor raised on protuberances . . . . . ***R. caespitosum s.lat.***

For South Australia, the entry for *Grasses of South Australia* (Jessop *et al.* 2006) becomes:

9. Palea narrow-lanceolate and usually much exceeding the sinus **9a**

9: Palea broadly obovate to oblanceolate, only shortly exceeding the sinus **10**

9a. Hair-tufts of the lower row next to the central rib absent, remaining tufts very dense, raised on distinct protuberances . . . . . ***R. robertsoniae***

9a: Hair-tufts of the lower row next to the central rib complete or, if absent, then remaining tufts not very dense nor raised on protuberances . . . . . ***R. caespitosum s.lat.***

This key also requires modification at couplet 4 to avoid confusing *R. robertsoniae* with *R. laeve*:

4. Lemma without a complete row of tufts above the callus **4a**

4: Lemma with a complete row of tufts above the callus **5**

4a. Remaining tufts sparse or absent . . . . . ***R. laeve***

4a: Remaining tufts dense and raised on distinct protuberances . . . . . ***R. robertsoniae***

which numbered about 230. She spent considerable effort trying to isolate subspecies of *R. caespitosum*, but was unable to do so, even though she found 'extreme forms' that she deemed worthy of taxonomic distinction, considering the level of delineation between other species already described in the genus.

If Robertson (unpubl.) was correct, and there are ten or more recognizable forms of *R. caespitosum*, 230 specimens may simply not have been enough to enable Vickery to identify any but a few specimens of the most common forms. At the time of writing, there were 4,403 specimens of *R. caespitosum* in Australian Herbaria (AVH 2018), which is a substantial increase over the number of specimens available to Vickery in 1956. This increase has enabled me to locate enough specimens from dry areas to establish consistent characters and describe *R. robertsoniae*. The distinctive features of *R. robertsoniae*, and its wide distribution across four states, including both sides of the Nullarbor, would suggest that it is a separate species of some antiquity.

A numerical morphological analysis applied to a larger and more geographically even data-set may enable the identification of other forms of *R. caespitosum* that warrant taxonomic recognition.

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Nomenclatural notes and typifications in Australian species of Paliureae (Rhamnaceae)

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Abstract: The nomenclature of the four species of *Ziziphus* Mill. and the one species of *Hovenia* Thunb. occurring in Australia is reviewed, including the role of the Hermann Herbarium for the typification of *Z. oenopolia* (L.) Mill. and *Z. mauritiana* Lam. Lectotypes are chosen for *Z. quadrilocularis* F.Muell. and *Z. timoriensis* DC. A key to species is provided, as well as illustrations for *Z. oenopolia*, *Z. quadrilocularis* and *H. dulcis* Thunb.

Keywords: Nomenclature, typification, *Hovenia*, *Ziziphus*, Rhamnaceae, Paliureae, Paul Hermann, Carolus Linnaeus, Henry Trimen, Australia

Introduction

Rhamnaceae tribe Paliureae Reissek ex Endl. was reinstated by Richardson *et al.* (2000b), after the first molecular analysis of the family (Richardson *et al.* 2000a). It consists of three genera, *Hovenia* Thunb., *Paliurus* Tourn. ex Mill. and *Ziziphus* Mill., which until then were assigned to the tribes Rhamneae Horan. (*Hovenia*) and Zizypheae Brongn. (= Paliureae; *Paliurus* and *Ziziphus*; Suessenguth 1953). This new tribal classification was confirmed in the analyses of Hauenschild *et al.* (2016, 2018). Two of the genera are present in Australia: *Hovenia* and *Ziziphus*.

The four species of *Hovenia* (POWO 2020) are distributed in south-east Asia from India, through Bhutan, Nepal and Myanmar to China, Japan and Korea. The genus was last reviewed by Kimura (1939) and Suessenguth (1953), followed by regional treatments, e.g. for China (Chen & Schirarend 2007), India (Sen Gupta & Safui 1984) and Japan (Noshiro 1999). The cultivated species *Hovenia dulcis* Thunb. is sparingly naturalised in Australia (Harden 1990).

Until recently, *Ziziphus* was regarded as a genus distributed throughout the tropics and warm dry regions of the world (Medan & Schirarend 2004). Islam & Simmonds (2006) recognised that there are two distinct clades of *Ziziphus*, one from the Americas and one from Europe, Africa and Australasia. Following a more detailed analysis, Hauenschild *et al.* (2016) reinstated *Sarcomphalus* P.Browne for the New World taxa and removed two species close to the unrelated *Condalia* Cav. (tribe Rhamneae) to the new genus *Pseudoziziphus* Hauenschild. The redefined *Ziziphus* is now a genus of c. 65 species (Mabberley 2017), occurring in Europe, Africa, south Asia, Melanesia and Australia. Three species are native to northern Australia, and one further species, *Z. mauritiana* Lam., is introduced. The last worldwide overview of the genus was published by Suessenguth (1953). Since then, only regional treatments and revisions have been published, most notably by Johnston (1963, 1964, 1972), Bhandari & Bhansali (2000), Chen & Schirarend (2007) and Cahen *et al.* (in press). For Australia, the genus as a whole was last reviewed by Bentham (1863), with subsequent regional treatments by Wheeler (1992) and Rye (1997) for the Kimberley region, Western Australia, and Bailey (1899) and Stanley & Ross (1986) for Queensland.

In preparation for the *Flora of Australia* treatment of Rhamnaceae, the nomenclature and typification of the species of *Ziziphus* and *Hovenia* occurring in Australia are clarified and discussed in this paper.

The synonymies of the widespread species *H. dulcis*, *Z. mauritiana* and *Z. oenopolia* (L.) Mill. only list names that have been used in Australia (APC 2020; APNI 2020). All types have been examined, unless indicated by "*n.v.*"; those that were seen online via JSTOR Global Plants and other herbarium websites are indicated by "photo seen".

The holotype designations by Johnston (1972) are here accepted if no other specimens of the type could be found; if there are several specimens then Johnston's listing of a "holotype" is interpreted as lectotypification (an error to be corrected, according to Art. 9.10; Turland *et al.* 2018; see also McNeill 2014). These can be accepted, as Johnston (1972) clearly indicated that he accepted the type specimens; also, at the time of writing, Johnston was not required to state "here designated" after type designations (Art. 7.11).

Identification keys and notes on the five species are also provided, as well as line-drawings of *H. dulcis*, *Z. oenopolia* and *Z. quadrilocularis* F.Muell., a taxon that does not seem to have been illustrated before.

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Key to genera of Paliureae in Australia

1. Leaves with 3 nerves, oblique; stipules persistent, often growing into spines; infructescence axes not thickened; fruit a dry-fleshed drupe . . . . . ***Ziziphus***

1: Leaves penninerved, symmetric; stipules caducous; infructescence axes thickened, fleshy; fruit a capsule . . . . . ***Hovenia***

Nomenclature

Rhamnaceae trib. **Paliureae** Reissek ex Endl.

Gen. Pl. 1095 (1840). — **Type:** *Paliurus* Mill.

Rhamnaceae trib. Zizypheae Brongn., *Énum. Pl. Mus. Paris* 122 (1843). — **Type:** *Ziziphus* Mill.

Ziziphus Mill.

Gard. Dict. abridg. ed. 4 [not paginated] (1754). — **Type:** *Z. jujuba* Mill., *nom. cons.*, *fide* Britton & P.Wilson, *Sci. Surv. Porto Rico* 5: 535 (1924). ≡ *Rhamnus zizyphus* L. ≡ *Ziziphus zizyphus* (L.) H.Karst., *nom. rej.* (see Kirkbride *et al.* 2006; Brummitt 2009; Wiersema *et al.* 2020).

Etymology. Derived from the Greek ζιζυφον (*zízyphon*), which originated from the Phoenician *zizuf* (Paclt 1999), the name for the lotus or jujube tree, *Ziziphus lotus* (L.) Lam.

The original spelling of the genus name is *Ziziphus*. A common and widely used orthographic variant of the name is "*Zizyphus*", which "appears to be more correct philologically, [...] but it is not permissible under the Rules to make orthographic corrections based *solely* on philological grounds" (Sprague 1929: 52). The rejection of a recent proposal by Paclt (1999) to conserve the name "*Zizyphus*" with that spelling confirms this assessment (Brummit 2000).

Note. *Ziziphus jujuba* Mill. has been recorded from Australia, but probably in error due to Lamarck's synonym for *Z. mauritiana* (viz. *Z. jujuba* (L.) Lam., which has often been confused with *Z. jujuba* Mill.); it is widely cultivated throughout the drier tropics and is occasionally found in cultivation in Australia, but seems not to have naturalized.

1. *Ziziphus oenopolia* (L.) Mill.

Gard. Dict. ed 8 [not paginated] *Ziziphus* no. 3 (1768), as "*oenoplia*". — *Rhamnus oenopolia* L., *Sp. Pl.* 194 (1753). — **Type citation:** "Habitat in Zeylonia ♄" Linnaeus also quotes the following references: "*Fl. Zeyl.* 88 *", "*Burm. zeyl.* 131. t. 61". **Lectotype:** Ceylon, *Herb. Hermann* 3: 46, no. 88 (BM000621972 & BM000621973; photos seen), *fide* Trimen, *J. Linn. Soc., Bot.* 24: 137 (1887), *non* P.I.Forster, *Austrobaileya* 3: 563 (1991), *nec* Wadhwa, *Revis. Handb. Fl. Ceylon* 10: 367 (1996).

Ziziphus celtidifolia DC., *Prodr.* 2: 20 (1825). — **Type citation:** "in ins. Timor". **Holotype:** Timor (G-DC, annotated "Museum de Paris 1821"; photo seen, IDC Micro-Edition 500, fiche 277).

Ziziphus rufula Miq., *Fl. Ned. Ind.* 1(1): 643 (1856), as "*Zizyphus*". — **Type citation:** "in Herb. Horsf.", "Java, tusschen de struiken in Bogor". **Type** not located (possibly K). Synonym *fide* Benth., *Fl. Austral.* 1: 412 (1863).

Ziziphus oligantha Merr. & L.M.Perry, *J. Arnold. Arbor.* 20: 338 (1939) (as "*Zizyphus*"). — **Type citation:** "British New Guinea: Western Division, Mabaduan, *Brass 6488* (type), April, 1936"; the authors also state: "The types [...], unless otherwise stated, are deposited in the herbarium of the Arnold Arboretum" (p. 324). **Holotype:** Mabaduan, Western Province, Papua New Guinea, Apr. 1936, *L.J. Brass 6488* (A00051554). **Isotypes:** BM000838645, BRI-AQ0317638, G00440946, K000723081, L0013808; photos seen (see also P.I.Forster, *Austrobaileya* 3: 563, 1991).

Spelling & etymology. The original spelling of the name in the first edition of *Species plantarum* is "*Rhamnus oenopolia*" (Linnaeus 1753: 194), but in the 10th edition of Vol. 2 of *Systema naturae*, Linnaeus (1759: 938) spelt the epithet "*oenopia*". In the second edition of *Species plantarum* (Linnaeus 1763: 282) and the 12th edition of *Systema naturae* (1767, vol. 2: 180), the author used the

Key to species of *Ziziphus* in Australia

1. Leaves distinctly discolorous, densely and closely greyish-pubescent beneath (W.A., N.T., Qld) . . . . . 2. ***Z. mauritiana***

1: Mature leaves ±concolorous, glabrous or sparsely pubescent beneath

2. Young stems and buds with numerous prominent, pale lenticels; tall rainforest tree (Qld: MacIlwraith Range) . . . . . 3. ***Z. timoriensis***

2: Young stems and buds without prominent lenticels; small trees, scrambling shrubs or lianes

3. Leaves thin-textured; flowers in apparent lateral clusters; carpels 2; fruits 6–8 mm long (N.T., Qld, Torres Strait islands) . . . . . 1. ***Z. oenopolia***

3: Leaves thick; flowers in distinct zig-zag rhipidia; carpels 3 or 4; fruits 14–26 mm long (W.A., N.T.) . . . . . 4. ***Z. quadrilocularis***

spelling "*oenoplia*". This evolution of the spelling of the name has already been noted by Richter (1840). It is not clear whether Linnaeus intended to correct the spelling of the name, or if these are merely printers' errors, which then were perpetuated. Subsequent editions, which were issued after Linnaeus' death, continued to use the latter spelling. When Miller (1768) transferred the species to *Ziziphus*, he did it with the same spelling, as "*Ziziphus oenoplia*"; this is one of the main reasons for the continued use of the epithet "*oenoplia*".

Gunawardena (1968: 54) and Quattrocchi (2012: 4013) state that the name is derived from the Greek *οίνος* (*oinos*), wine, and *πλείων* (*pleion*), full, many. Trimen (1893: 280) states that "[I]t is difficult to conceive what Linnaeus intended by applying this term to the present species which has nothing vinous about it in any way." Certainly, "*oenoplia*" would be a more correct way of forming a compound epithet from these two Greek words. However, classical and Renaissance Latin also uses the term "*oenopolium*" for a wine shop or tavern (Peck 1898; Berkowitz *et al.* 1994: 44), and it is not inconceivable that Linnaeus derived the specific epithet from that word. While the species certainly has dark berries that resemble grapes, it is not known if Linnaeus had actually seen fruiting specimens; hence the reasons for his choice of epithet remain uncertain.

Because of the uncertainties in the spelling of the name in Linnaeus's own publications and because we can only speculate about the correct etymology of the name, the best option seems to be to continue to use the original spelling (see also Forster 1991).

***Typification of* Rhamnus oenopolia.** Forster (1991) and Wadhwa (1996) both published lectotypifications of the name *Rhamnus oenopolia*. However, these authors overlooked the publication by Trimen (1887), who already designated a type for the name.

Linnaeus first described this species in *Flora Zeylanica* (1747), under the genus *Rhamnus* as no. 88, using a short diagnostic phrase, as this was before he applied the binomial system. In this book Linnaeus published the results of his examination of the herbarium of Paul Hermann, which was collected in Ceylon in the late 17th century. The herbarium is bound in five volumes and now held in the Natural History Museum, London (BM); other Hermann herbaria in Gotha (Rauschert 1970), Leiden (van Oostroom 1937) and Paris (Lourteig 1966) were not examined by Linnaeus (Jarvis 2007). In his *Species plantarum*, Linnaeus (1753) published the species under the name *Rhamnus oenopolia*. In both publications, he also quoted a plate from Burman (1737).

Trimen (1887) provided determinations for all specimens in the Hermann Herbarium, and noted that:

- In the Hermann Herbarium at the Natural History Museum, Linnaeus himself added to Hermann's labels a reference to the species number in *Flora Zeylanica* (1747)
- In *Species plantarum* (1753), for species previously described in *Flora Zeylanica*, "Linnaeus was careful to quote under them the numbers of the 'Fl. Zeylan.,' and thus *the specimens of Hermann's Herbarium become types* for many of Linnaeus's species" (Trimen 1887: 130; my emphasis)
- Trimen's list of the Hermann Herbarium is in two columns: the first gives the species number in *Flora Zeylanica* and the binomial used for it in *Species plantarum*; the second column contained his "*determinations of the type specimen or specimens* representing the species in Hermann's herbarium" (Trimen 1887: 133; my emphasis)
- In most cases the "Hermann *specimens* should determine what was the plant intended by Linnaeus rather than his book references" (Trimen 1887: 133).

This means that Trimen has effected lectotypification for those names for which only one gathering (even if more than one specimen) is being referred to (Art. 9.15, Turland *et al.* 2018; see also McNeill 2014). This corresponds with Jarvis (2007), where specimens or illustrations from the Hermann Herbarium are generally deemed to be types of names in Linnaeus' *Flora Zeylanica*.

While Trimen is credited for providing a comprehensive list of the specimens in the Hermann collection, his indication of "types" of the species described by Linnaeus from that herbarium seems to have generally been overlooked (Jarvis 2007). However, there is no reason to disregard Triemen's typifications, especially if other pre-type-method typifications are generally accepted, such as the typification of many genera and sections in Pfeiffer (1871–1875).

In the case of *Rhamnus oenopolia*, Trimen (1887: 137) states: "88. Rhamnus Œnoplia, Sp. 194 . . Ziziphus Œnoplia, Mill.". On p. 46 of Vol. 3 of the Hermann Herbarium there are two separate branches, each annotated "88". They are glued to the pages of the book in such a way that the top specimen shows the upper surface of the leaves and the bottom specimen shows the lower surface. Tony Orchard, then Australian Botanical Liaison Officer at Kew, examined and photographed the *Ziziphus* specimens at BM. His conclusion was that the two branches were collected from the same plant at the same time, as they look very similar and are at the same stage of development. As such, the lectotypification of Trimen can be accepted.

Not being aware of Trimen's publication, Forster (1991) lectotypified the species with a plate in Burman's *Thesaurus Zeylanicus*, which Linnaeus referenced when describing the species. While Linnaeus describes the illustration as "*bona*", i.e. well executed (Linnaeus 1747: 36), a specimen is preferable as type. Wadhwa (1996) indicated a specimen in Linnaeus' Herbarium (LINN 262.33) as the type (with "type" being correctable to "lectotype"; Art. 9.10). Both are original material and possible syntype specimens, but Trimen's publication has priority.

Fig. 1. A–D *Ziziphus oenopolia*: **A** habit ×0.7; **B** lower surface of leaf ×4; **C** flower ×8; **D** fruit ×0.7. **E–H** *Z. quadrilocularis*: **E** habit ×0.7; **F** lower surface of leaf ×4; **G** flower ×8; **H** fruit ×0.7. **I–K** *Hovenia dulcis*: **I** habit ×0.7; **J** lower surface of leaf ×4; **K** flower ×8. — A–B *W.E. Cooper 1444* (MEL2150696), C *G.M. Wightman 4148* (MEL1603351), D *C.R. Dunlop 8391* (MEL0227920), E–G *G.J. Leach 2318* (MEL0221006), H *J.H. Willis s.n.* (MEL1534533), I–K *H. Idzumi & M. Togashi s.n.* (MEL2439813). Illustration by Anita Barley.

The two branches of the lectotype on p. 46 have later received separate BM numbers and barcodes. As they form part of the same gathering, both branches are here accepted as the lectotype (similar to a multi-sheet specimen; see Art. 8.3).

Note. *Ziziphus oenopolia* occurs in the Top End of the Northern Territory and on Cape York Peninsula from the Torres Strait islands south to Princess Charlotte Bay (Qld), in drier rainforests and vine thickets from sea level to c. 120 m. Outside Australia, it is distributed from India to south-east Asia and China. **Fig. 1A–D.**

2. *Ziziphus mauritiana* Lam.

Encycl. 3: 319 (1789). — **Type citation:** "Isle de France". **Lectotype:** "Isle de France" [Mauritius], *P. Sonnerat s.n.* (P-LA; IDC Micro-Edition 6207, no. LM-128/18), *fide* M.C.Johnst., *Fl. Trop. E. Africa Rhamnac.* 29 (1972). **Isolectotype:** G-DC (IDC Micro-Edition 500, fiche 277).

Rhamnus jujuba L., *Sp. Pl.* 1: 194 (1753); *Z. jujuba* (L.) Gaertn., *Fruct. Sem. Pl.* 1: 203 (1788), *nom illeg.*; *Z. jujuba* (L.) Lam., *Encycl.* 3: 318 (1797), *nom. illeg.*, *non* Gaertn. (1788), *nec* Mill., *Gard. Dict. Ed. 8.* [not paginated] *Ziziphus* no. 1 (1768). — **Type citation:** "Habitat in India. ♄.". Linnaeus also quotes the following references: "*Fl. Zeyl.* 89 *", "*Pluk. alm.* 199. *Raj. dendr.* 44". **Lectotype:** Ceylon, *Herb. Hermann 3.14 no. 89* (BM00621844 & BM00621845; photos seen), *fide* Trimen, *J. Linn. Soc., Bot.* 24: 137 (1887), *et* Wadhwa, *Revis. Handb. Fl. Ceylon* 10: 369 (1996). **Remaining syntypes:** BM00621466, BM00621467 & BM00621468 (photos seen).

Rhamnus mauritiana P.Willemet, *Herb. Maurit.* 20 (1796) & *Ann. Bot. (Usteri)* 18: 20 (1796). — **Type citation:** "Habitat in Mauritiae frequens in sylvis: au Pouce, aux plaines St Pierre, &c.". **Type:** not located (the whereabout of Willemet's herbarium are unknown; Stafleu & Cowan, *Taxon. Lit. ed. 2*, 7: 314, 1988). Synonym *fide* Afr. Pl. Database (2020) & Arbonnier, *Arbres, Arbustes & Lianes Afr. Ouest ed. 4*, 762 (2019).

Ziziphus tomentosa Poir. in Lam., *Encycl. Suppl.* 3: 192 (1813); *Ziziphus poiretii* G.Don, *Gen. Hist.* 2: 26 (1832), as "*poiretti*", *nom. illeg. & superfl.* — **Type citation:** "Ile de Saint-Domingue. ♄ (*V.s. in herb Desfont.*)". **Lectotype:** "Santo Domingo I., *Poiteau*" (P, *n.v.*), *fide* M.C.Johnst., *Fl. Trop. E. Afr. Rhamnac.* 29 (1972). **Isolectotype:** St. Dominigue, *P.A. Poiteau* (G-DC; IDC Micro-Edition 500, fiche 277).

Ziziphus orthacantha DC., *Prodr.* 2: 21 (1825); *Ziziphus mauritiana* var. *orthacantha* (DC.) A.Chev., *Rev. Int. Bot. Appl. Agric. Trop.* 27: 477 (1947). — **Type citation:** "in Senegalia. Bacle.". **Holotype:** Senegal, *C.H. Bacle s.n.* (G-DC, IDC Micro-Edition 500, fiche 277), *fide* M.C.Johnst., *Fl. Trop. E. Afr. Rhamnac.* 29 (1972).

Ziziphus rotundata DC., *Prodr.* 2: 21 (1825). — **Type citation:** "♄ in ins. Mauritiae sylvis [...] v.s. ex h. mus. Par.". **Holotype:** Ile de France [Mauritius] et de Bourbon [Réunion], *s.coll.* (G-DC, labelled "Museum de Paris"; IDC Micro-Edition 500, fiche 277), *fide* M.C.Johnst., *Fl. Trop. E. Afr. Rhamnac.* 29 (1972).

Ziziphus aucheri Boiss., *Diagn. Pl. Orient.* sér. 1, 2: 5 (1843). — **Type citation:** "Hab. In *Persiâ australi* circa *Bouchir*", *P.M.R. Aucher-Eloy 4320*. **Lectotype:** "Iran, Bushir [Bouchir], *Aucher 4320*" (G, *n.v.*), *fide* M.C.Johnst., *Fl. Trop. E. Afr. Rhamnac.* 29 (1972). **Isolectotypes:** FI006688, K01818560, P000681965 (photos seen). Synonym *fide* Afr. Pl. Database (2020) & Arbonnier, *Arbr. Arbust. & Lianes Afr. Ouest ed. 4*, 774 (2019).

Ziziphus jujuba var. *stenocarpa* Kuntze, *Rev. Gen. Pl.* 1: 121 (1891). — **Type citation:** "Cultivirt Delhi". **Holotype:** India, Delhi, cult. ♄ 30', 15 July 1875, *C.E.O. Kuntze 7241* (NY00415103, photo seen).

Ziziphus jujuba var. *fruticosa* Haines, *Forest Fl. Chota Nagpur* 270 (1910). — **Type citation:** "Singbhum, Manbhum, usually in waste open places, railway embankments, etc.". **Type:** not located (possibly K, where the main part of H.H. Haines' herbarium is deposited). Synonym *fide* M.C.Johnst., *Fl. Trop. E. Afr. Rhamnac.* 29 (1972).

Paliurus mairei H.Lév., *Repert. Spec. Nov. Regni Veg.* 12: 535 (1913); *Ziziphus mairei* (H.Lév.) Browicz & Lauener, *Notes Roy. Bot. Gard. Edinburgh* 27: 281 (1967), *nom. illeg.*, *non* Dode, *Bull. Soc. Bot. France* 55: 649 (1909). — **Type citation:** "Yun-Nan: brousse, rives du fleuve Bleu, juillet 1912. 400 m (E.E. Maire)". **Holotype:** Yun-Nan: brousse, rives du fleuve Bleu, altit. 400 m, July 1912, *E.E. Maire s.n.* (E00275332, photo seen). **Isotype:** A00249937 (photo seen; 3 leaves and 1 immature fruit with photo of holotype, distributed by E in 1928).

Ziziphus mauritiana var. *deserticola* A.Chev., *Rev. Int. Bot. Appl. Agric. Trop.* 27: 477 (1947). — **Type citation:** "Colonie du Niger : de Tahoua a Agades (Chev. n° 43 302) Type!". **Type:** not located (possibly P). Synonym *fide* J.-P.Lebrun & Stork, *Enum. Pl. Fleurs Afr. Trop.* 2: 190 (1992).

***Typification of* Rhamnus jujuba.** Jarvis (2007: 791) states that "Johnston (1972) indicated Herb. Hermann material (BM) as type. Although there is material in more than one volume, it appears to have been part of a single gathering. Consequently, this is accepted as the first typification (Art. 9.15) [now Art. 9.17; Turland *et al.* (2018)], with the choice subsequently restricted by Wadhwa [1996]."

While Johnston (1972: 29) indicated "*Hermann 89* (BM, holo.!)" as the type, the same was already done by Trimen (1887), who wrote "89. Rhamnus Jujuba, Sp. 194 . . . . Zizyphus Jujuba, *Lam.*" and clearly indicated the type of the name to be no. 89 of the Hermann Herbarium in London (see explanation under *Z. oenopolia* above).

The following material of no. 89 is present in that herbarium: Vol. 1, p. 71, has three branches glued onto the page (labelled "a", "b" and "c"); Vol. 3, p. 14, consists of two branches, which are glued on one sheet (together with *Nephrodium unitum* (L.) Bory and *Tragia involucrata* L.; Jarvis 2016); Vol. 5, p. 99, is an illustration of the species.

Wadhwa (1996: 369) gave the type as "*Hermann* 3: 14. n. *89* (BM)". As such, he published a second-step lectotypification, as explained by Jarvis (2007). Later the two branches have received separate BM numbers. As with *Z. oenopolia*, both branches are here accepted as the lectotype specimen. Note that, in error, Jarvis (2007) cites the barcode number of *Nephrodium unitum* (BM000594656) under *Rhamnus jujuba*. The other specimens and the illustration in Vol. 3 and Vol. 5 of the Hermann Herbarium are original material and syntypes of the name.

Note. *Ziziphus mauritiana* is introduced in Australia (Grice 2002), occurring scattered in woodlands and vine thickets in the drier parts of northern Australia from Derby (W.A.) to Maryborough (Qld), usually in disturbed areas adjacent to settlements; it is sometimes cultivated. The species is widespread from tropical Africa through the Middle East, India, south-east Asia and China; it is also present in the Caribbean and parts of the Americas.

3. *Ziziphus timoriensis* DC.

Prodr. 2: 20 (1825). — **Type citation:** "In insula Timor". **Lectotype (designated here):** Timor, [1803,] *J.B.L.T. Leschenault de la Tour s.n.* (G-DC, with annotation: "Museum de Paris 1821"; IDC Micro-Edition 500, fiche 277). **Isolectotypes:** P00298039 (with annotation: "Ziziphus timoriensis DC. prod."), P00298040 (photos seen).

Rhamnaceae sp. (=RFK/25814) B.Hyland & Whiffin, *Austral. Trop Rain Forest Trees* 1: 112, 129, 182, Code 1055 (1993).

Typification. Candolle (1825) only indicated where the type specimen was collected, but after consulting his herbarium in Geneva, it is clear that the species was described from a specimen collected by Leschenault, who was in Timor in Apr. 1803 (George 2009). Two other collections in Paris are most likely duplicates. The specimen from Candolle's herbarium is in good condition and is chosen as the lectotype.

Note. The species occurs in the MacIlwraith Range, Qld, in rainforest at 250–400 m. It is also native to Timor, Sulawesi and the Moluccas.

4. *Ziziphus quadrilocularis* F.Muell.

Fragm. 3: 57 (1862) (as "*Zizyphus*"). — **Type citation:** "Ad ripas rupestres fluvii Victoriae. F.M." — **Lectotype (designated here):** Victoria River, W.A., Jan. & Mar. 1856, *F. Mueller s.n.* (MEL712594, branch on left hand side). **Residual syntypes:** Victoria River, W.A., Jan. & Mar. 1856, *F. Mueller s.n.* (MEL712594, fruit and infertile branch). Upper Victoria River, W.A., Jan 1856, *F. Mueller s.n.* (K000723079).

Typification. The type specimen at MEL is clearly mixed, as two collection dates are listed on the label. Presumably the earlier collecting date (Jan. 1856) is for the flowering branch on the left hand side of the sheet, and the later date (Mar. 1856) refers to collection of the fruit, which is present in the packet, and possibly the infertile branchlet on the right-hand side. The fruit is cut open and displays the 4-locular ovary that gave the species its name; however, both 3- and 4-locular ovaries are common in this plant. The flowering branch is selected as lectotype.

The syntype at the Royal Botanic Gardens, Kew, is only labelled with the earlier date (Jan. 1856), but contains two flowering branches and one fruiting branch, which must have also been collected later. It is not clear if this is a duplicate of the MEL sheet, as the location is slightly different.

Note. *Ziziphus quadrilocularis* grows in the western Kimberley region and from Mabel Downs (W.A.) to Arnhem Land (N.T.), in vine thickets and savannah woodlands from sea level to c. 360 m. **Fig. 1E–H.**

Hovenia Thunb.

Nov. Gen. Pl. 1: 7 (1781). — **Type:** *H. dulcis* Thunb.

Etymology. Named in honour of David ten Hoven, Dutch official of the City of Amsterdam and sponsor of Thunberg's travels to Japan (Théis 1810).

1. *Hovenia dulcis* Thunb.

Nov. Gen. Pl. 1: 8 (1781). — **Type citation:** "Crescit prope Nangasaki". **Lectotype:** Japan [Aug. 1775–Nov. 1776], *C.P.Thunberg s.n.* (UPS-THUNB V-005733; photo seen), *fide* Sengupta & Safui, *Bull. Bot. Surv. India* 26(1-2): 54 (1984). **Syntypes:** LINN-HS398-1 (labelled "Thunb. Japon."; photo seen), S11-13034 (labelled "Habitat in Japonia. Specimen ibi lectum ex Upsalia misit Exp. DD. Thunberg, a. 1780"; photo seen), SBT12364 (labelled "e Jáponia. Thunberg" and "Hovenia dulcis. Thunb. Fl. jap." in Thunberg's hand; photo seen). **Possible syntype:** LD1731646 (labelled "Jap."; photo seen).

Typification. Thunberg's own herbarium at Uppsala (UPS) is generally seen to be the source of his type specimens (Stafleu & Cowan 1986). Sen Gupta & Safui (1984), after carefully examining the Microfiche edition of the herbarium, listed "*Thunberg* s. n. (UPS)" as location of the "holotype". This is here accepted as lectotypification of the name, since only one specimen of *H. dulcis* is present in Thunberg's herbarium (Juel 1918; Ebihara *et al.* 2015–).

There are also specimens in other herbaria, these are listed here as syntypes. While they look very similar, it cannot be ascertained if they are duplicates of the lectotype. The specimen at Lund (LD) is not labelled with the collector's name but the LD database lists Thunberg as possible collector.

Note. The species is introduced in Australia and occasionally adventive on rainforest margins in New South Wales and possibly Queensland. It is native to China, Korea and Japan. **Fig. 1I–K.**

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Clarification of the type locality of *Amanita peltigera* (Agaricales, Amanitaceae), phylogenetic placement within subgenus *Amanitina*, and an expanded description

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Abstract: In the protologue of *Amanita peltigera* D.A.Reid the type locality is stated as Stirling West, Western Australia, but no such place exists. Both collector information and rainfall records for the relevant period indicate the type locality is in South Australia not Western Australia. A comparison of collections of *A. peltigera* from Kangaroo Island, South Australia, with collections from the southwest of Western Australia shows they form a single clade without a clear geographic distribution among its subclades. *Amanita peltigera* falls within the recently recognised section *Arenariae*. An amended and expanded description of *A. peltigera* is provided.

Keywords: Fungi, mushrooms, Basidiomycota, Australia

Introduction

Derek Reid, a mycologist from Kew, visited Australia between May and July 1976 with the aim of preparing a monograph for the Australian Biological Resources Study on the mushroom genus *Amanita* Pers. He visited Western Australia (W.A.), South Australia (S.A.) and Victoria, working with mycologists in those states. He examined type material held in Australian herbaria and made additional collections. On his return to Kew he reviewed all types of Australian *Amanita* spp. and prepared the monograph, which included 46 taxa and a key. There were several new species, including *A. peltigera* D.A.Reid (Reid 1980).

He described *A. peltigera* as a distinctive species with a greyish cap with conspicuous whitish peltate remnants of universal veil, a saccate volva, no partial veil and subglobose to very broadly elliptic, amyloid spores (Fig. 1A). Although he did not place it within a subgenus or section, this combination of amyloid spores and saccate volva, would have placed it in subgenus *Lepidella* (E.-J. Gilbert) Veselý *emend.* Corner & Bas, and either section *Phalloideae* (Fr.) Quél. or in section *Amidella* (E.-J. Gilbert) Konrad & Maubl. (Corner & Bas 1962). In the protologue, the collection locality is Stirling West, W.A., the collector is J. Randals, and the collection date March 1976 (Reid 1980). However, there is nowhere called Stirling West in W.A. Also, rainfall in early 1976 for both Perth (close to the City of Stirling) and Albany (close to the Stirling Range) would not have been heavy enough to trigger a flush of mushrooms in March (Bureau of Meteorology 2018). The annotation on the type packet is Stirling West, Australia (Fig. 1B), and as Stirling West, S.A. had 122 mm of rain 25–29 February 1976 (Bureau of Meteorology 2018) this is a more likely type locality. On the packet the collector is given as John Randals (Fig. 1B); at that time, John Randles, who lives in Stirling West and works at the Waite Institute, Adelaide, S.A., collected mushrooms for its mycological herbarium (J. Randles, pers. comm., 4 Feb. 2018). It appears the correct annotation should be Stirling West, S.A., collector J. Randles, March 1976. The type locality is therefore about 2500 km east of where it is stated in Reid (1980).

The southwest of W.A. has a rich, endemic flowering plant flora, which has been separated from south eastern Australia by increasing aridity, beginning in the Oligocene/Miocene about 33.9 million years before the present (Hopper & Gioia 2004). This isolation, however, has not been continuous, with connectivity between the southwest of W.A. and S.A. including Kangaroo Island, during a period of low sea level and relatively high rainfall in the Pleistocene, between 50 000 and 30 000 years ago (Bowler 1980). These wetter periods would

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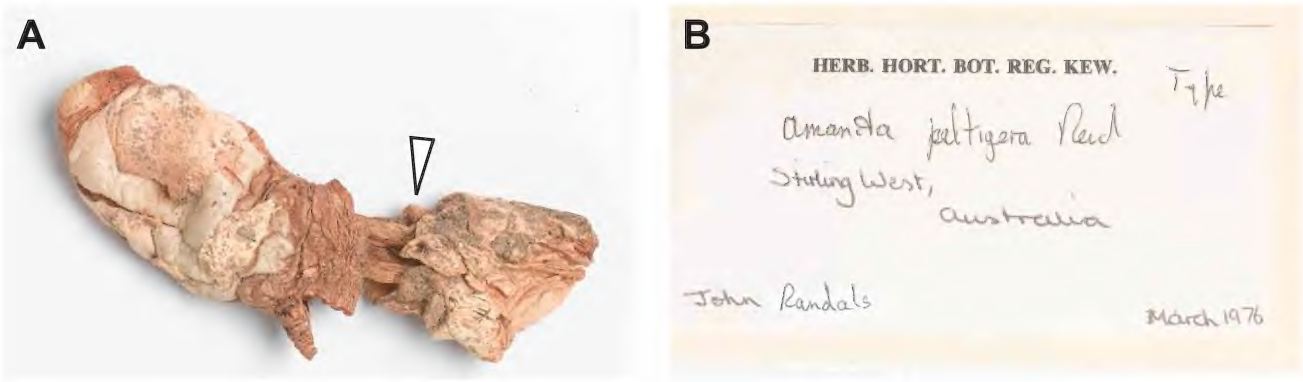

Fig. 1. Type of ***Amanita peltigera***, K(M) 236385. **A** Collection, the arrow indicates the saccate volva. **B** Packet. Images: J. Percy-Bower, Western Australian Herbarium.

have assisted colonisation and migration along this coastal corridor, whilst the subsequent periods of relative aridity would have contracted species distributions (Boomsma & Lewis 1980).

As most *Amanita* spp. are mycorrhizal symbionts of woody plants (Cui *et al.* 2018), they may have evolved at the same rate as their hosts, forming a fungal flora unique to the southwest of W.A. Alternatively, there may be disjunct populations of *Amanita* spp. across southern Australia. Two collections which fitted the description of *A. peltigera* were made by EMD from forested areas in the southwest of W.A. in 2011 and 2015. The realisation in 2018 that the type locality was in S.A., not W.A., raised the possibility that these collections might not be *A. peltigera* but a similar species which could be separated geographically. On the other hand, collections from W.A. and S.A. might represent disjunct populations of the same species.

The genus *Amanita* is monophyletic (Cui *et al.* 2018), with species defined by the field character of a membranous or friable volva (universal veil), and microscopic and ontogenetic characters of bilateral gill trama, acrophysalidic stipe trama, and schizohymenial development (Bas 1969). In the past, two characters, spore amyloidy and a sulcate pileus margin, were used to characterise two subgenera: *Amanita* and *Lepidella* (Corner & Bas 1962). More recently, molecular sequencing, particularly of non-mycorrhizal species from the most 'primitive' part of the genus *sensu* Bas (subgenus *Lepidella*, section *Lepidella*, subsection *Vittadiniae* Bas; Wolfe *et al.* 2012), has prompted a re-assessment of whether *Amanita* should be split, and if so, how this should be done. Vizzini *et al.* (2012), supported by Redhead *et al.* (2016), have split *Amanita* into two sister genera *Amanita s.str.* and *Saproamanita* Redhead, Vizzini, Drehmel & Contu, a decision which has not been universally accepted (Tulloss *et al.* 2016). The most recent taxonomic treatment of *Amanita* by Cui *et al.* (2018) has provided another interpretation, based on concatenated 28S nuclear ribosomal large subunit rRNA (nuLSU), translation elongation factor 1-α (*ef1-α*), RNA polymerase II (*rpb2*) and β-tubulin (*β-tubulin*) sequences. They have divided *Amanita* into three subgenera: *Amanita*, *Amanitina* (E.-J.Gilbert) E.-J.Gilbert, and *Lepidella* Beausigneur, all with good support. Subgenus *Amanitina* contains most of the species that were included in subgenus *Lepidella sensu* Bas (1969), apart from subsection *Vittadiniae sensu* Tulloss *et al.* (2016), which is placed in subgenus *Lepidella*. Subgenus *Amanitina* is subdivided into six sections: *Amidella*, *Arenariae* Zhu L.Yang, Yang-Yang Cui & Qing Cai, *Phalloideae*, *Roanokenses* Singer ex Singer, *Strobiliformes* Singer ex Zhu L.Yang, Yang-Yang Cui & Qing Cai and *Validae* (Fr.) Quél. This treatment has merit because it is consistent with molecular phylogeny and has been accepted by He *et al.* (2019); it has been followed in this paper.

There are three aims in this paper. Firstly, we determine the placement of putative collections of *A. peltigera* from S.A. and W.A. within subgenus *Amanitina* using nuLSU sequences. Secondly, we compare cloned nuclear ribosomal internal transcribed spacer (ITS) sequences, and other sequences, of putative *A. peltigera* collections from S.A. with those from W.A. We have also included collections in this comparison which are macroscopically similar, but with a more persistent partial veil. Lastly, as our genetic comparisons showed that all these collections formed a well-supported clade, even though they were not identical and could not be separated geographically, we provide an amended and expanded description of *A. peltigera*.

Materials and methods

Taxonomy. Methodology is largely based on that of Tulloss (c. 2000). Colour names, including the colour of spores in deposit and other shades of white to cream (designated by the letter A–G), follow Royal Botanic Garden, Edinburgh (1969) while colour codes are from Kornerup & Wanscher (1983). In the descriptions of basidiospores (and basidia) the notation [x/y/z] denotes x basidiospores measured from y basidiomes from z collections. Biometric variables for spores follow Tulloss (c. 2000), i.e. "**L** = the average spore length computed for one specimen examined and the range of such averages, **L'** = average spore length computed for all spores measured, **W** = the average spore width computed for one specimen examined and the range

Table 1. GenBank numbers for nuLSU sequences, including type species, from the different sections of *Amanita* subgenus *Amanitina*. Sequences in bold have been generated for this work.

Section	*Amanita* sp.	Voucher number	Location	Collector	Date	nuLSU
Amidella	*A. volvata* (Peck) Lloyd	KA12-1367	Gyeongbuk, Korea		6 Sep 2012	KF245907
	A. brunneomaculata Zhu L.Yang, Y.Y.Cui & Q.Ca	HKAS 70032	Yunnan, China	Qing Cai	29 Jul 2011	MH486411
	A. lanigera Y.Y.Cui, Q.Cai & Zhu L.Yang	HKAS 89030	Yunnan, China	Gang Wu	9 Jul 2014	MH486621
	A. parvicurta Y.Y.Cui, Q.Cai & Zhu L.Yang	HKAS 101215	Yunnan, China	Zhu L. Yang	30 Aug 2017	MH486745
Arenariae	*A. arenaria* (O.K.Mill. & E.Horak) Justo	PERTH07586329, VPI679 (type collection)	City of Albany, W.A.	O.K. Miller	22 Jun 1989	GQ925382
	A. wadulawitu McGurk, E.M.Davison & E.L.J.Watkin	PERTH09144404	City of Melville, W.A.	E.M. & P.J.N. Davison	26 Apr 2015	**MN918100**
	A. wadulawitu	PERTH09144382	Shire of Esperance, W.A.	K.J. Knight	29 Mar 2018	**MN918101**
Phalloideae	*A. phalloides* (Vaill. ex Fr.) Link	HKAS75773	China			JX998060
	A. djarilmari E.M.Davison	PERTH08776067	Shire of Cuballing, W.A	E.M. & P.J.N. Davison	18 Apr 2016	KY977704
	A. marmorata	PERTH08690596	Shire of Denmark, W.A.	K. Syme	8 May 2014	KY977711
Roanokenses	*A. roanokensis* Coker	FLAS-F-60892	Florida, USA	R. Healy, B. Kaminsky, D. Borland, N. Kraisitudomsook	14 Jun 2017	MH620252
	A. carneiphylla O.K.Mill.	PERTH08793530	City of Melville, W.A.	E.M. & P.J.N. Davison	8 May 2016	**MN911351**
	A. preissii (Fr.) Sacc	PERTH 8690766	Kings Park, W.A.	N.L. Bougher	25 Jun 2015	KY290654
Strobiliformes	*A. strobiliformis* (Paulet ex Vittad.) Bertill.	MB-001177	Germany			MH486895
	A. cinereopannosa Bas	RET 318-8	Maine, USA			HQ539678
	A. aspericeps Y.Y.Cui, Q.Cai & Zhu L.Yang	HKAS 77783	Guangdong, China	Fang Li	13 Sep 2012	MH486372
	A. cinereoradicata Y.Y.Cui, Q.Cai & Zhu L.Yang	HKAS63641	Yunnan, China	Jiao Qin	10 Jul 2010	MH486452
Validae	*A. excelsa* (Fr.) Bertill.	HKAS96169	Austria			MH486492
	A. flavoconia G.F.Atk.	BW_PH22	Massachusetts, USA			HQ539693
	A. citrina Pers.	BW JLR 102106-1	New Jersey, USA			HQ539679
Amanita	*A. subglobosa* Zhu L.Yang (outgroup)	HKAS58837	China	Q. Cai	29 Aug 2009	JN941152
	A. peltigera	PERTH08793514	Shire of Manjimup, W.A.	E.M. & P.J.N. Davison	3 Jun 2013	**MN900625**
	A. peltigera	PERTH09138560	Shire of Mundaring, W.A.	E.M. & P.J.N. Davison	30 Jul 2015	**MN900626**
	A. peltigera	PERTH08793581	Shire of Serpentine-Jarrahdale, W.A.	E.M. & P.J.N. Davison	15 Jun 2016	**MN900627**
	A. peltigera	AD282185	Kangaroo Island, S.A.	J.F. Haska	16 May 2015	**MN900628**

Table 2. GenBank numbers for ITS clones, *ef1-α* and *rpb2* gene regions for putative collections of *Amanita peltigera* from W.A. and S.A. and other species from section *Arenariae*. Sequences in bold have been generated for this work.

Amanita sp.	Voucher number	Location	Collector	Date	GenBank numbers		
					ITS	*ef1-α*	*rpb2*
A. peltigera	PERTH08467625	City of Armadale, W.A.	E.M. & P.J.N. Davison	10 Jun 2011	**MN894291–MN894294**		
A. peltigera	PERTH08793492	Shire of Manjimup, W.A.	E.M. & P.J.N. Davison	1 Jun 2013	**MN894295–MN894302**		
A. peltigera	PERTH08793514	Shire of Manjimup, W.A.	E.M. & P.J.N. Davison	3 Jun 2013	**MN894303–MN894307**	**MN909824**	**MN912054**
A. peltigera	PERTH09138560	Shire of Mundaring, W.A.	E.M. & P.J.N. Davison	30 Jul 2015	**MN894322–MN894326**	**MN909825**	**MN912055**
A. peltigera	PERTH08793581	Shire of Serpentine-Jarrahdale, W.A.	E.M. & P.J.N. Davison	15 Jun 2016	**MN894317–MN894321**	**MN909826**	**MN912056**
A. peltigera	AD282184	Kangaroo Island, S.A.	J.F. Haska	2 Jun 2015	**MN894312–MN894316**	**MN909828**	**MN912058**
A. peltigera	AD282185	Kangaroo Island, S.A.	J.F. Haska	16 May 2015	**MN894308–MN894311**	**MN909827**	**MN912057**
A. wadjukiorum	PERTH08793522	City of Melville, W.A.	E.M. & P.J.N. Davison	23 Jul 2014		**MN928569**	**MN928570**
A. wadulawitu	PERTH09144404	City of Melville, W.A.	E.M. & P.J.N. Davison	26 Apr 2015		**MN928566**	**MN928560**
A. wadulawitu	PERTH09144382	Shire of Esperance, W.A.	K.J. Knight	29 Mar 2018		**MN928567**	**MN928561**
A. wadulawitu	PERTH09144390	Shire of Serpentine-Jarrahdale, W.A.	E.M. & P.J.N. Davison	30 May 2018		**MN928565**	**MN928562**
A. djarilmari (outgroup)	PERTH08776067	Shire of Cuballing, W.A.	E.M. & P.J.N. Davison	18 Apr 2016	KY977732	MF000750	MF000755

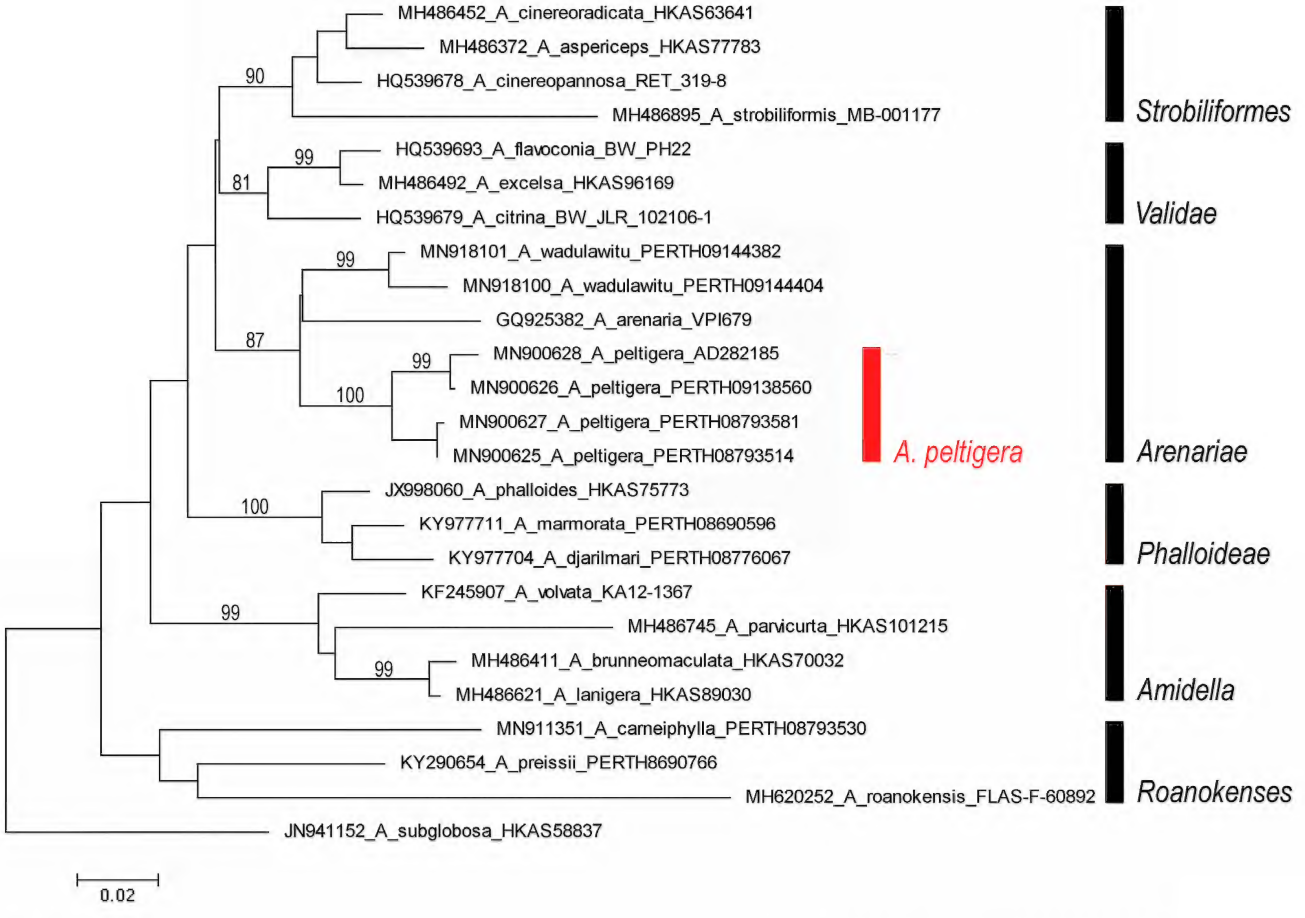

Fig. 2. Molecular phylogenetic analysis by maximum likelihood method of nuLSU sequences from species from all sections in subgenus *Amanitina*. The tree is rooted in *Amanita subglobosa* (subgenus *Amanita* section *Amanita*). Each section is highlighted in black and putative *A. peltigera* collections in red. All bootstrap values less than 80% have been deleted.

Table 3. Percentage differences in the internal transcribed spacer (ITS) region within collections and among collections of at least four cloned sequences from putative *Amanita peltigera* collections.

	No. clones	AD282185	PERTH 08467625	PERTH 09138560	PERTH 08793492	PERTH 08793514	PERTH 08793581	AD282184
AD282185	4	0.7–5.8						
PERTH08467625	4	2.8–5.7	0.7–2.8					
PERTH09138560	5	2.8–5.1	0.7–2.5	0.3–2.3				
PERTH08793492	8	9.7–12.1	9.5–11.5	9.6–11.6	0.2–3.5			
PERTH08793514	5	8.6–10.7	8.2–10.0	8.5–10.4	0.8–4.3	0.5–2.2		
PERTH08793581	5	8.7–11.0	8.7–10.3	8.7–10.6	1.0–3.8	0.5–2.8	0.7–3.3	
AD282184	5	10.5–13.4	10.3–12.4	10.3–12.5	8.1–10.5	7.0–9.2	7.3–9.6	0.2–1.8

of such averages, **W'** = average spore width computed for all spores measured, Q = the length/breadth for a single spore and the range of the ratio of length/breadth for all spores measured, **Q** = the average value of Q computed for one specimen examined and the range of such averages, **Q'** = the average value of Q computed for all spores measured". Author citations follow *Index Fungorum* (2019). Herbarium codes follow *Index Herbariorum* (2019).

Phylogenetics. DNA extraction, amplification and cloning of the ITS (ITS1 + 5.8S + ITS2) region, amplification of the nuLSU, *ef1-α*, *rpb2* and *β-tubulin* regions follow the methodology of Davison *et al.* (2017a). Sequence data were assembled with Geneious version 10.0.5 (Geneious 2005–2016). Additional sequences were accessed from *GenBank* (2019) (Tables 1 and 2).

Phylogenetic analyses were conducted with MEGA version 5 (Tamura *et al.* 2011). Maximum likelihood trees were built of the nuLSU, ITS, *ef1-α*, *rpb2* and concatenated *ef1-α* and *rpb2* gene regions. The best model for each dataset was determined using the Model Function in MEGA. The Hasegawa-Kishino-Yano model (Hasegawa *et al.* 1985) with gamma distributed rates was used for the nuLSU gene region, the Tamura 3-parameter model (Tamura 1992) with invariant sites was used for the ITS gene region, the Kimura 2-parameter model (Kimura 1980) with gamma distributed rates was used for the *ef1-α* gene region, with invariant sites for the *rpb2* gene region, and with gamma distributed rates for concatenated *ef1-α* and *rpb2* gene regions. Bootstrap consensus support was inferred from 500 replicates.

Results

Placement of putative *Amanita peltigera* collections within subgenus *Amanitina*

The nuLSU is the only gene region available from GenBank for all of the type species from the six sections within subgenus *Amanitina*. These, together with additional species, have been used to determine the affinities of *A. peltigera* within the subgenus (Table 1). Phylogenetic analysis by the maximum likelihood method (808 base pair positions) shows the *A. peltigera* collections form a clade with good support, within section *Arenariae* (Fig. 2).

Comparison of ITS and other gene regions from S.A. and W.A. collections

ITS. The ITS region is between 593 and 603 base pairs long for the seven collections of *A. peltigera* (Table 2). The ITS amplicon produced for each collection was cloned and at least four clones sequenced. Within a collection the difference between clones is 0.2–5.8% (Table 3). Between collections the difference is up to 13.4%. Phylogenetic analysis by the maximum likelihood method (578 base pair positions) shows there are three clades, two of which have good bootstrap support (Fig. 3). The collection AD282184 from S.A. has the least variation in its clones. Two of the four clones from AD282185 from S.A. fall within one of the W.A. clone clades.

Other gene regions. Additional gene regions (*ef1-α* and *rpb2*) are available for some of the putative *A. peltigera* collections and two other members of section *Arenariae* (*A. wadulawitu* McGurk, E.M.Davison & E.L.J.Watkin and *A. wadjukiorum* E.M.Davison) (Table 2). Phylogenetic analysis by the maximum likelihood method of the *ef1-α* (473 base pair positions) and *rpb2* (637 base pair positions) gene regions separately, and concatenated (1111 base pair positions), shows the putative *A. peltigera* collections cluster in a well-supported clade (Fig. 4).

Comparison of ITS, ef1-α and rpb2 phylogenies. The *ef1-α*, *rpb2* and concatenated phylogenies show all putative *A. peltigera* collections form a well-supported clade (Fig. 4). Within this clade there are two sub-clades and a singleton which are also apparent in the ITS phylogeny (Fig. 3, Table 3). These sub-clades are not clearly separable geographically, and may not be consistent macroscopically. For example, AD282184, is a singleton in the ITS, *rpb2* and concatenated phylogenies (Figs. 3 and 4) and

the partial veil is not apparent (Fig. 5A). The other collection from S.A. (AD282185) clusters with collections PERTH08467625 and PERTH09138560 from W.A. with good support in the ITS, *ef1-α*, *rpb2* and concatenated phylogenies (Figs. 3 and 4); two of these collections have a partial veil which disappears very early (Fig. 5B). Collections PERTH08793492, PERTH08793514 and PERTH08793581 from W.A. form a well-supported sub-clade in the ITS, *ef1-α*, *rpb2* and concatenated phylogenies (Figs. 3 and 4); in these collections there is a somewhat more persistent partial veil (Fig. 5C).

As no sequences are available from the type collection, K(M) 236385, we cannot say for certain which of these lineages is representative of the type. The type description makes no mention of a partial veil, and none is apparent on the specimen. However, as this may not exclude the early loss of the partial veil, we provide an emended and expanded description of *A. peltigera* based on our collections from S.A. and W.A.

Amended and expanded description of *Amanita peltigera*

Amanita peltigera D.A.Reid

Vict. Naturalist 95(2): 49 (1978). — **Holotype:** Australia. South Australia: Stirling West, 35°00' S, 138°43' E, Mar. 1976, *John Randles s.n.*; K(M) 236385!

Mycobank number: MB308577.

Pileus 12–70 mm wide, to 10 mm thick, pale smoke grey to pale vinaceous buff to milky coffee to drab to hazel to sepia (4C2–E2–5B2–D4–6B3–D2–D4–E5–E6–7E5) occasionally virgate, margin paler, without surface staining or bruising, initially convex becoming plane with decurved margin and slightly depressed centre, surface slightly tacky when moist shiny when dry; margin non-striate, slightly appendiculate when young. *Universal veil on pileus* adnate, felted to membranous, as one or several patches in centre of disc or absent, white. *Lamellae* adnate to adnexed to free, close to subcrowded, white to B (pale 4A2), 2–7 mm broad, margin concolorous, fimbriate; *lamellulae* frequent to infrequent in several lengths, shortest

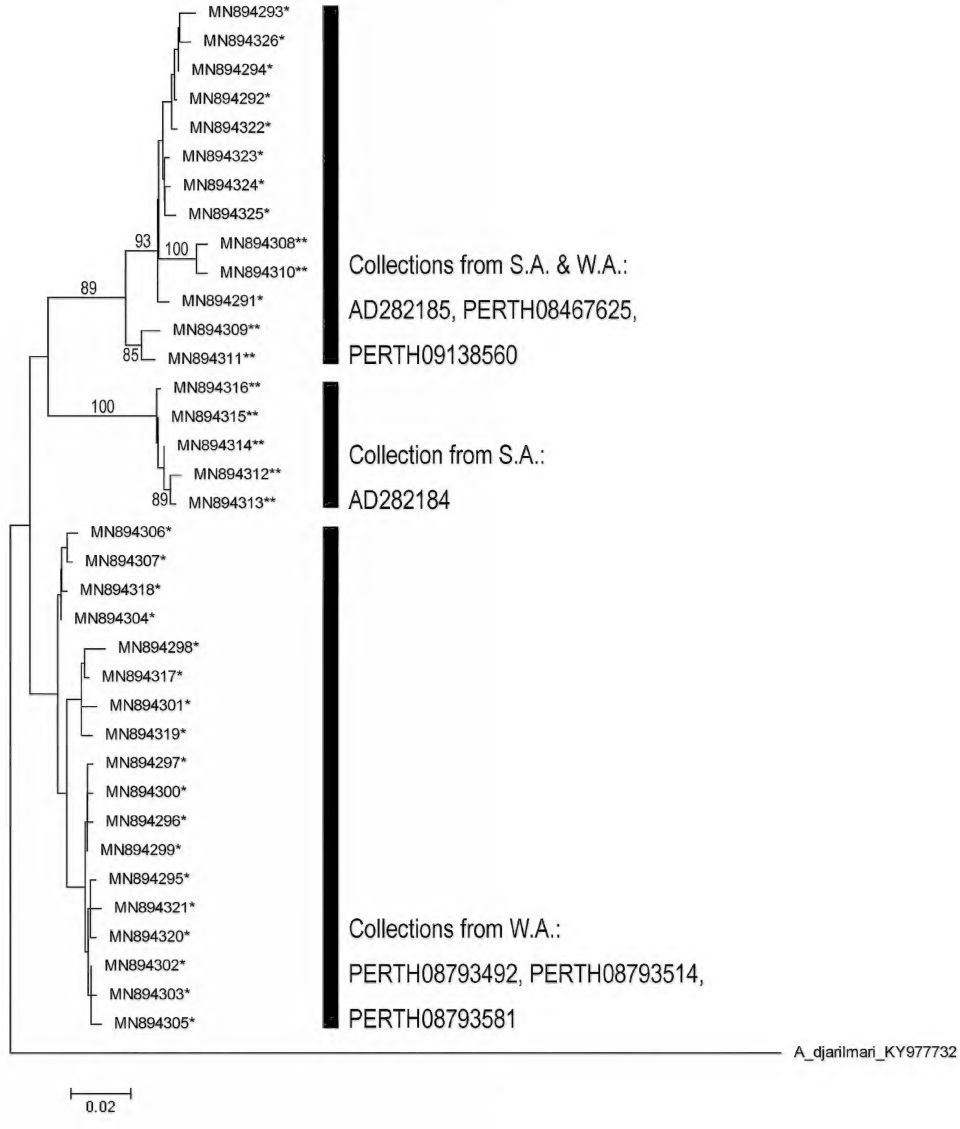

Fig. 3. Molecular phylogenetic analysis by maximum likelihood method of ITS clones from *Amanita peltigera* collections from S.A. and W.A. The tree is rooted in *Amanita djarilmari*. All bootstrap values less than 80% have been deleted. Key: * sequences from collections from W.A.; ** sequences from collections from S.A.

truncate or rounded truncate, longest attenuate. *Stipe* 23–85 mm long, 5–16 mm wide, cylindrical or tapering upwards, white, surface smooth or minutely floccose or fibrillose. *Partial veil* apical to superior, descendent, flaring, thin, striate above, persistent or fugacious or not observed, white. *Bulb* 7–30 × 7–25 mm, globose or ovoid or ellipsoid, white. *Remains of universal veil* at top of bulb saccate, forming a thin or thick free limb to 15 mm high, white. *Pileus and stipe context* white unchanging, stipe solid becoming hollow. *Smell* none. *Spore deposit* white. **Fig. 5.**

Basidiospores [499/25/25] (6.5–) 8–10.5 (–11.5) × (5.5–) 6–8 (–9) µm, (**L** = 8.0–10.0 µm; **L'** = 9.1 µm; **W** = 6.3–7.7 µm; **W'** = 7.1 µm; Q = (1.06–) 1.14–1.43 (–1.62); **Q** = 1.20–1.38; **Q'** = 1.29), colourless, thin-walled, smooth, amyloid, sub-globose to broadly ellipsoid to ellipsoid, contents monoguttulate; apiculus sublateral, cylindric, c. 1 × 1 µm, truncate or rounded.

Pileipellis to 350 µm thick in old specimens, with a colourless gelatinised suprapellis to 250 µm thick and yellowish brown or brown subpellis; filamentous hyphae 2–10 µm wide, thick-walled, walls hyaline, gelatinising, contents yellowish brown to brown often granular, radially orientated sometimes sinuous; inflated cells very infrequent, to 10–15 µm wide; vascular hyphae infrequent to frequent, 2–15 µm wide, occasionally branched, pale yellowish brown. *Pileus context* filamentous hyphae less frequent, equal or dominant, 2–35 µm wide, with widest constricted at septa, thin walled, colourless or very pale brown; inflated cells to 350 × 50 µm thin-walled some gelatinising, clavate or ventricose or cylindrical or ovoid, colourless; vascular hyphae very infrequent to infrequent, 2–10 µm wide, occasionally branched, pale yellowish brown *Lamella trama* bilateral, divergent. *Central stratum* comprising 5–12% of distance between bases of basidia on opposing hymenial surfaces, of thin-walled, colourless, filamentous hyphae, 3–15 µm wide; inflated cells not observed; vascular hyphae very infrequent, 3–7 µm wide, branches not observed, pale yellow. *Subhymenial base* with angle of divergence 10°–30° from central stratum with filamentous hyphae following smooth broad curve to subhymenium, of dominant or equal thin-walled, colourless, frequently

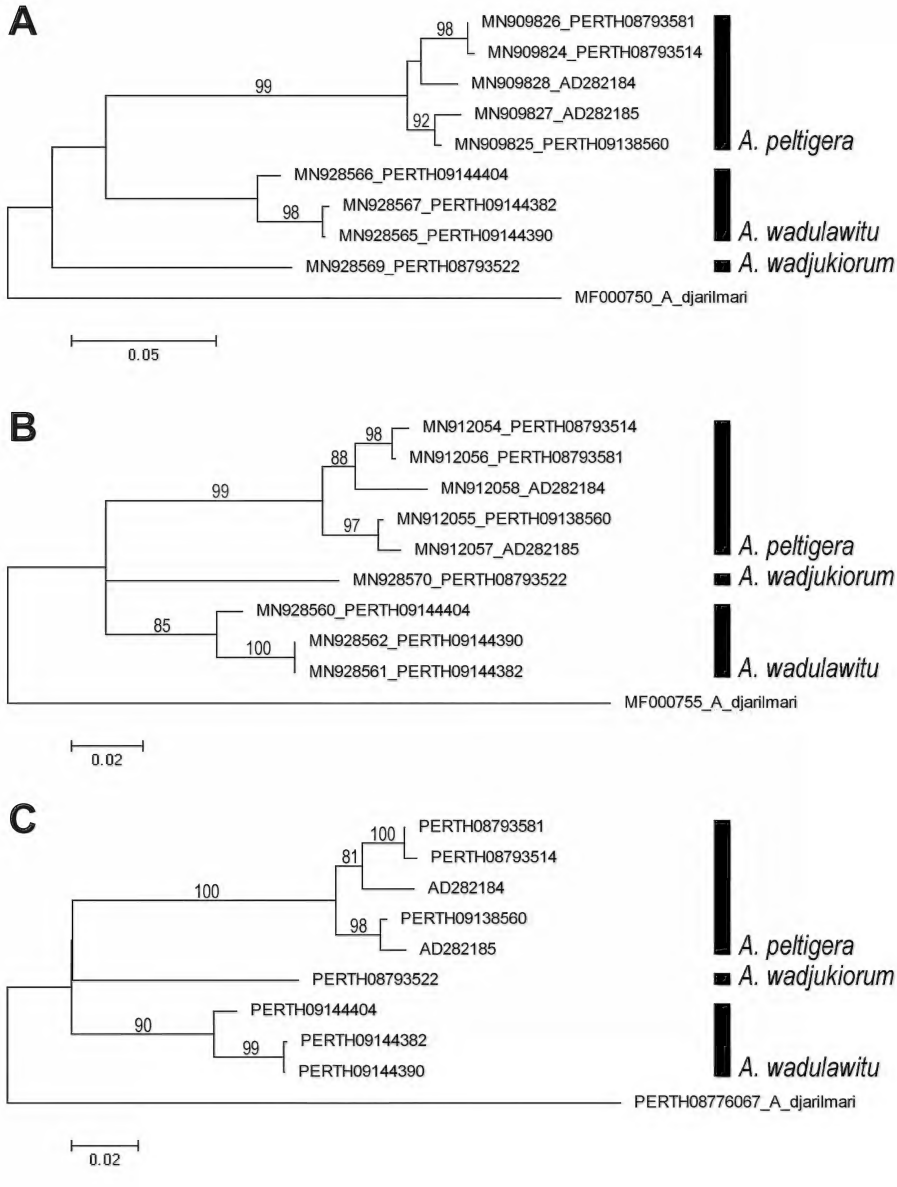

Fig. 4. Molecular phylogenetic analysis by the maximum likelihood method of putative *Amanita peltigera* collections from S.A. and W.A. with *A. wadulawitu* and *A. wadjukiorum* from section *Arenariae*. **A** *ef1-α* gene region. **B** *rpb2* gene region. **C** Concatenated sequences of *ef1-α* and *rpb2* gene regions. The trees are rooted in *Amanita djarilmari*. All bootstrap values less than 80% have been deleted.

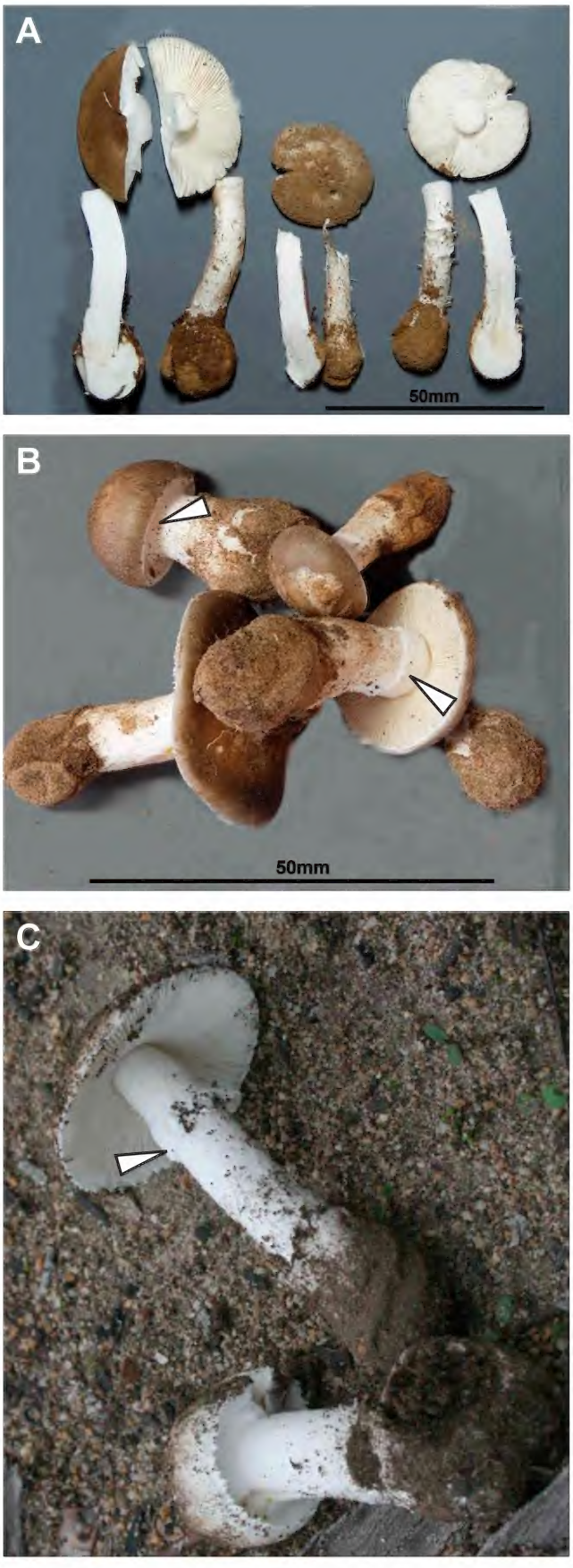

Fig. 5. ***Amanita peltigera*** collections showing differences in the partial veil. **A** AD282184 in which the partial veil is not apparent. **B** AD282185 where there is a partial veil (arrow) which disappears early. **C** PERTH08793514 has a somewhat more persistent partial veil (arrow) which disappears early. — Photos: A, B J.F. Haska, C E.M. Davison.

branched filamentous hyphae 2–25 µm wide, widest close to subhymenium and constricted at septa; inflated cells frequent to equal, colourless, to 200 × 35 µm, clavate, cylindrical, ventricose, ovoid, ellipsoid, terminal occasionally intercalary; vascular hyphae infrequent, 2–7 µm wide, occasionally branched, colourless or pale yellow. *Subhymenium* with basidia arising terminally from barely inflated to pyriform terminal segments, to 20 µm wide. *Lamella edge tissue* sterile, with inflated cells infrequent to frequent, 30–50 × 7–15 µm, clavate, pyriform capitate, ovoid or cylindrical, colourless, some disarticulating. *Basidia* [380/19/19] (25–) 34–54 (–63) × (8–) 9–15 (–16) µm, thin-walled, colourless, c. 82% 4-spored, c. 8% 3-spored, c. 10% 2-spored, c. <1% 1-spored, sterigmata to 8 × 2 µm. *Universal veil on pileus* not layered, with elements periclinal or irregularly disposed; filamentous hyphae dominant, 2–25 µm wide, colourless, gelatinising, occasionally disarticulating; inflated cells infrequent to frequent, ovoid (to 130 × 110 µm), clavate (to 200 × 35 µm), spherical (to 120 × 120 µm), ellipsoidal (to 130 × 75 µm) or ventricose (to 160 × 35 µm), terminal, colourless, gelatinising; vascular hyphae very infrequent to frequent, 2–20 µm wide, occasionally branched, pale yellow. *Universal veil on stipe base inner layer* narrow, only found in some basidiomes, axial orientation; filamentous hyphae 3–8 µm wide, thick-walled, colourless, gelatinising, often puzzle-like; inflated cells very infrequent spherical (to 90 × 90 µm) or clavate (to 80 × 20 µm); vascular hyphae not observed. *Universal veil on stipe base outer layer* wide, with axial orientation; filamentous hyphae dominant or equal, 2–12 µm wide with occasional segments to 25 µm wide, thick-walled, colourless, gelatinising; inflated cells infrequent to equal, ovoid (to 100 × 90 µm), clavate (to 300 × 90 µm), spherical (to 75 × 75 µm), ellipsoidal (to 260 × 45 µm) or ventricose (to 140 × 45 µm), terminal, colourless, gelatinising; vascular hyphae infrequent, 2–10 µm wide, occasionally branched, colourless or pale yellow. *Stipe context* longitudinally acrophysalidic; filamentous hyphae 2–12 µm wide, colourless, gelatinising; acrophysalides dominant, clavate (to 400 × 35 µm) or cylindrical (to 270 × 40 µm), terminal, colourless, gelatinising; vascular hyphae infrequent to frequent, 2–20 µm wide, occasionally branched, pale yellow or pale yellowish brown. *Partial veil* not examined. Clamp connections not observed in any tissue. **Fig. 6.**

Diagnostic features. Very small to medium-sized fruiting bodies which have a pale grey to vinaceous buff to sepia pileus, which is paler at the margin. The universal veil is white, felted to sub-membranous, forming one or several patches in the centre, or it may be missing. The gills are white to ivory white; the stipe is white with a white, superior, partial veil that disappears early or may be absent. The bulb is globose, ovoid or ellipsoid; the universal veil at the top of the bulb is white and forms a free limb. The flesh is white and unchanging throughout. There is no distinctive smell. The spores are amyloid and subglobose to broadly ellipsoid to ellipsoid. The universal veil on

both the pileus and at the stipe base is composed of dominant hyphae and frequent, large inflated cells. Clamp connections are absent.

Distribution and habitat. Gregarious in sand, sandy clay and lateritic gravel, in native vegetation; nearby plants include *Allocasuarina fraseriana*, *A. muelleriana*, *A. verticillata*, *Banksia marginata*, *B. menziesii*, *Corymbia calophylla*, *Eucalyptus baxteri*, *E. cladocalyx*, *E. cneorifolia*, *E. cosmophylla*, *E. diversicolor*, *E. diversifolia*, *E. globulus*, *E. marginata*, *E. obliqua*, *E. patens*, *E. remota*, *E. rudis*, *E. wandoo*, *Gastrolobium bilobum*, *Jacksonia furcellata*, *J. horrida*, *Leptospermum continentale*, *Melaleuca uncinata*, *Taxandra parviceps*, *Xanthorrhoea semiplana*. Occurs in the Swan Coastal Plain Perth SWA02, Northern Jarrah Forest JAF01, Southern Jarrah Forest JAF02, Warren WAR01, Mount Lofty Ranges FLB01 and Kangaroo Island KAN01 IBRA subregions (Department of the Environment 2013).

Fruiting period. April to June.

Other specimens examined

WESTERN AUSTRALIA. Shire of Waroona, 30 May 1995, *N.L. Bougher E5385* (PERTH07551568); City of Armadale, 10 June 2011, *E.M. Davison 14-2011 & P.J.N. Davison* (PERTH08467625) (ITS: MN894291–MN894294); Shire of Serpentine-Jarrahdale, 8 June 2003, *E.M. Davison 12-2003 & P.J.N. Davison* (PERTH08793441); 15 June 2016, *E.M. Davison 53-2016 & P.J.N. Davison* (PERTH08793581) (ITS: MN894317–MN894321, nuLSU: MN900627, *ef1-α*: MN909826, *rpb2*: MN912056, *β-tubulin*: MN905762); City of Cockburn, 5 May 2012, *E.M. Davison 12-2012 & P.J.N. Davison* (PERTH08793484); Shire of Manjimup, 1 June 2013, *E.M. Davison 23-2013 & P.J.N. Davison* (PERTH08793492) (ITS: MN894295–MN894302); 1 June 2013, *E.M. Davison 24-2013 & P.J.N. Davison* (PERTH08793506); 3 June 2013, *E.M. Davison 32-2013 & P.J.N. Davison* (PERTH08793514) (ITS: MN894303–MN894307, nuLSU: MN900625, *ef1-α*: MN909824, *rpb2* MN912054); Shire of Mundaring, 30 July 2015, *E.M. Davison 50-2015 & P.J.N. Davison* (PERTH09138560) (ITS: MN894322–MN894326, nuLSU: MN900626, *ef1-α*: MN909825, *rpb2*: MN912055); Shire of Waroona, 13 June 1995, *B. Dunstan E5451* (PERTH07552874); City of Armadale, 5 June 2006, *P. Robertson E8325* (PERTH07699867); City of Albany, 11 June 1991, *K. Syme 73/91* (PERTH03978516); 13 June 1991, *K. Syme KS 104/91 & M. Hart* (PERTH04162102); Shire of Manjimup, 3 May 2008, *K. Syme KS 2090* (PERTH08105340); Shire of Denmark, 23 May 2011, *K. Syme KS 2609 & A. Syme* (PERTH08720800).

SOUTH AUSTRALIA. Kangaroo Island, 11 June 2014, *J.F. Haska JHAR 538* (AD282187); 11 June 2014, *J.F. Haska JHAR 539* (AD282186); 16 May 2015, *J.F. Haska JHAR 627* (AD282185) (ITS: MN894308–MN894311, nuLSU: MN900628, *ef1-α*: MN909827, *rpb2*: MN912057, *β-tubulin*: MN905761); 23 May 2015, *J.F. Haska JHAR 654* (AD282184) (ITS: MN894312–MN894316, *ef1-α*: MN909828, *rpb2*: MN912058); 27 June 2015, *J.F. Haska JHAR 663* (AD282267); 6 Apr. 2016, *J.F. Haska JHAR 698* (AD282183); 6 May 2016, *J.F. Haska JHAR 723* (AD282182); 22 June 2016, *J.F. Haska JHAR 803* (AD282181); 17 May 2017, *J.F. Haska JHAR 956* (AD282180).

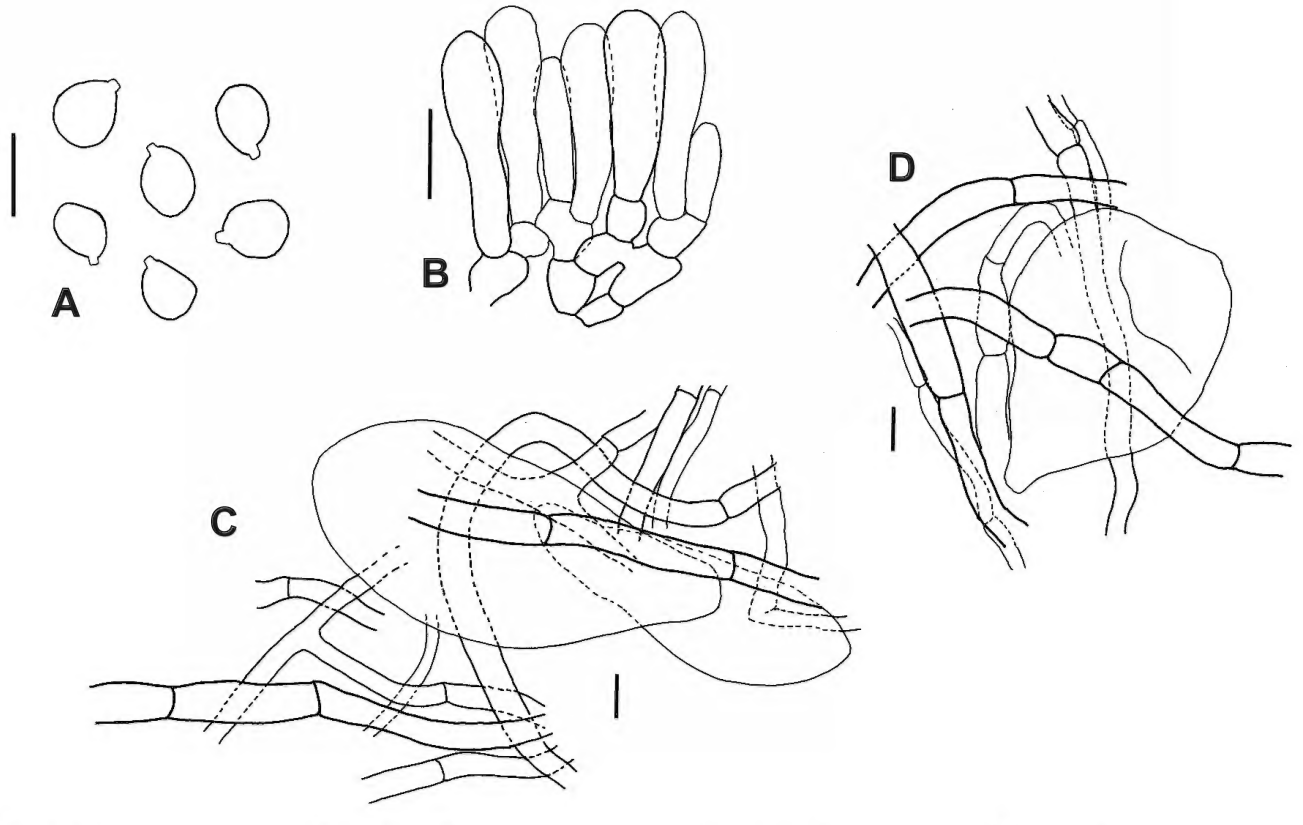

Fig. 6. Microscopic features of ***Amanita peltigera***, type collection K(M) 236385. **A** Basidiospores. **B** Basidia. **C** Universal veil from pileus, flake, unsquashed. **D** Universal veil from top of the bulb, gentle squash. — Scale bars: A, B = 10 µm, C, D = 50 µm.

Discussion

One of the aims of this paper was to determine the placement of *A. peltigera* within subgenus *Amanitina* according to the phylogeny and revised sectional taxonomy of Cui *et al.* (2018). It falls within the recently recognised section *Arenariae* (Fig. 2). The only other described members from this section (*A. lesueurii* E.M.Davison, *A. wadulawitu* and *A. wadjukiorum*) are all from southern Australia. This section may be a lineage which developed in Gondwana, similar to section *Amarrendiae* (subgenus *Amanita*), another Gondwanan lineage with species described from both Australia and Argentina (Truong *et al.* 2017).

Reid (1980) described *A. peltigera* as a distinctive species, however, he incorrectly stated the type locality as being in W.A. not S.A. In order to determine whether this species occurs in both states, we have compared the macroscopic appearance, micro-anatomy and molecular sequences of putative collections from both states. These comparisons have shown *A. peltigera* to be a widespread species in southern Australia which shows variation in the persistence of the partial veil.

The most widely used gene region for discriminating between species in the Basidiomycota is the ITS (Schoch *et al.* 2012), and Hughes *et al.* (2013) found that 97% of their agaric collections had less than 2% base pair divergence between haplotypes within an individual. Within *Amanita*, Cai *et al.* (2014) have shown ITS sequences are a valuable DNA barcode marker for species from section *Phalloideae*; however, our limited experience with ITS sequences from haplotypes of species from this section from southern Australia, is that they fail to discriminate between species which are morphologically distinct and geographically separated (Davison *et al.* 2017b). Haplotypes from other sections of *Amanitina* may be more variable, for example 23 haplotypes from five collections of *A. preissii* (section *Roanokenses*) showed differences of 0.16–3.65% (Davison *et al.* 2017a). The ITS sequences from haplotypes of the putative *A. peltigera* are even more variable, for example there is up to 5.8% in AD282185, whilst the variation between collections from different subclades is up to 13.4% (Table 3). However, the *ef1-α*, *rpb2* and concatenated phylogenies show putative *A. peltigera* collections form a well-supported clade (Fig. 4). It is on this basis that we have concluded *A. peltigera* is a species with a wide geographic range, but showing some variation in the partial veil (Fig. 5). *Amanita peltigera* is also reported from New South Wales (Wood 1997), Tasmania (Gates & Ratkowsky 2016) and Queensland (Atlas of Living Australia 2020); however, we have not studied these other collections.

The *A. peltigera* collections from Kangaroo Island are less than 200 km from Stirling West, the type locality. One of the two collections (AD282184, AD282185) from which we have obtained sequences could be designated an epitype (interpretative type). We have not done this, firstly, because the type, K(M) 236385, still exists and is identifiable, and secondly, because the variation within the Kangaroo Island collections means we are unsure which of these would be the most appropriate (Figs. 2–5, Table 3).

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A taxonomic review of the *Styphelia intertexta* group (Ericaceae: Epacridoideae: Styphelieae)

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Abstract: Species belonging to the Western Australian *Styphelia intertexta* group or Group III (*sensu* Puente-Lelièvre *et al.* 2016) are described, illustrated and their distributions mapped. The treatment includes descriptions of two new species, *S. deserticola* Hislop and *S. saxicola* Hislop, as well as updated descriptions for the two previously described species in the group, *S. intertexta* A.S.George and *S. subulata* (F.Muell.) Hislop, Crayn & Puente-Lel. The morphological attributes of the group are given and a key to species provided.

Keywords: *Styphelia*, Styphelieae, Ericaceae, taxonomy, *Styphelia intertexta* group, new species

Introduction

The *Styphelia intertexta* group (or Group III) is one of 12 natural groups resolved within the large *Styphelia* Sm.–*Astroloma* R.Br. clade of tribe Styphelieae Bartl., as a result of recent molecular research (Puente-Lelièvre *et al.* 2016). The group consists of just four species and is thought to be exclusively Western Australian. Morphological assessment suggests that it is unlikely that other western or eastern Australian taxa not included in previous molecular analyses belong here. In terms of their floral morphology, three of the four group members are *Styphelia* in the previously accepted sense of Brown (1810: 537) and Bentham (1868). That is, they have long exserted anthers and styles. *Styphelia subulata* (F.Muell.) Hislop, Crayn & Puente-Lel. is the exception in having anthers partially included in (or barely exserted from) the corolla tube together with a much shorter style; this being the most common floral configuration for the many species of axillary-flowered *Leucopogon* recently transferred to *Styphelia* (Crayn *et al.* 2020).

The two earlier described members of the group, *Styphelia intertexta* and *S. subulata*, are widespread and locally common, while the new species described below, *S. deserticola* Hislop and *S. saxicola* Hislop are more restricted and have conservation-coding (Smith & Jones 2018). Both are poorly known plants from remote, eremaean regions of Western Australia.

Following on from the recent taxonomic review of the *Styphelia xerophylla* group (Hislop & Puente-Lelièvre 2019), this paper provides a similarly comprehensive treatment of the small *S. intertexta* group detailing its morphological attributes and providing descriptions of its member species.

Methods

This study was based on examination of dried specimens housed at PERTH, together with field observations of the species described (excluding *Styphelia deserticola*) and their relatives in Western Australia.

Foliar measurements and observations were taken from dried specimens in natural posture. Care was taken to confine observations to mature leaves. Inflorescence length was measured from the point of attachment at the axil to the tip of the bud-rudiment. Floral measurements were taken from rehydrated flowers in natural posture, with the exception of the corolla lobes which were uncurled to their fullest length before measuring.

Bioregions referred to in the text and shown on distribution maps follow *Interim Biogeographic Regionalisation for Australia* (IBRA) v. 7 (Department of the Environment 2013).

Taxonomy

The *Styphelia intertexta* group

Morphological synopsis. *Leaves* helically arranged; apex long-mucronate, pungent; lamina adaxially convex, with strongly recurved to revolute margins; abaxial surface deeply grooved, hairy throughout or at least within the grooves. *Inflorescence* 2–3 (4)-flowered, flowers sessile; axis erect, extending above the uppermost floral node and terminating in a bud-rudiment; basal portion of axis, below the lowest fertile bract, somewhat compressed dorsiventrally, with usually 4 opposite and decussate sterile bracts; distal portion, above the uppermost fertile bract, sharply 3-angular. *Bracteoles* not striate, keeled,

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at least in the distal half. *Sepals* not striate, venation rarely conspicuous, longer or shorter than the corolla tubes. *Corolla* white or pale cream, the lobes sometimes partially tinged pink in bud. *Corolla tube* internal surface hairy below the lobes in the distal ¼–¾, external surface glabrous. *Corolla lobes* usually spreading from the base, revolute and coiled abaxially (in *S. subulata* spreading from a little above the base, and usually recurved only, occasional revolute and partially coiled); outer surface glabrous, inner surface densely hairy with twisted and ornamented hairs. *Filaments* terete, attached ½–⅔ above anther base, adnate to corolla tube just below the sinuses. *Anthers* usually long-exserted from the corolla tube and free from each other (partially included or occasionally barely exserted in *S. subulata*). *Ovary* glabrous, 5-locular, mid to dark green when dry. *Nectary* annular, ± truncate to variously lobed, often longitudinally grooved below the sinuses. *Style* usually glabrous and smooth throughout or occasionally hairy towards the base (populations with hairy styles are fairly common in *S. intertexta* and rare in *S. subulata*), usually long-exserted from the corolla tube (included in *S. subulata* and held at the throat), base abruptly differentiated from ovary apex, arising directly from ovary apex, not inset in a cylindrical depression. *Drupe* ellipsoid to ± globose, much longer than the calyx, circular in section, apex obtuse; mesocarp well-developed at maturity, gynophore absent.

Important distinguishing features. Western Australian taxa that have always been treated as *Styphelia* (i.e. those with long-exserted, free anthers and long-exserted styles) are grouped in four different parts of the phylogenetic tree obtained by Puente-Lelièvre *et al.* (2016). In addition to Group III, there are three taxa in Group II (*S. tenuiflora* Lindl., *S. melaleucoides* F.Muell. subsp. *melaleucoides* and subsp. *ovata* (Benth) Hislop, Crayn & Puente-Lel.) and two relatively isolated species, *S. hainesii* F.Muell. and *S. exserta* (F.Muell.) Sleumer. Members of the *S. intertexta* group can be readily distinguished from these by their leaf morphology, all species having strongly recurved to revolute leaf margins, deeply grooved and hairy abaxial leaf surfaces and long-mucronate, pungent leaf apices. *Styphelia tenuiflora*, *S. melaleucoides*, *S. hainesii* and *S. exserta* all have leaves that differ from this in various ways, and in particular none has the deeply grooved abaxial leaf surfaces. Further differences between Group III and Group II are the paler (usually white rather than cream-coloured) flowers of the former, and fruit that are ellipsoid or globose with a rounded apex rather than ovoid or ovoid-ellipsoid with a tapering sub-acute apex. *Styphelia hainesii* is further distinguished by its very large red flowers with a discrete band of hairs in the lower half of the internal corolla tube. Two significant distinguishing features of *S. exserta* are the partite nectaries and cylindrical, often curved fruit.

Styphelia subulata differs from the other members of Group III in having anthers partially included in the corolla tube (or occasionally barely exserted) and an included style (Fig. 6). For this reason it was first described as a *Leucopogon* R.Br., *L. subulatus* F.Muell. (Mueller 1864: 103). In the early 1990's, long after that name had been erroneously synonymised by Bentham (1868) under *L. insularis* DC., the species was recognised again by the Western Australian Herbarium under the phrase name *Leucopogon* sp. Kau Rock (*M.A. Burgman 1126*).

The different presentation of the style and anthers make *Styphelia subulata* easy to recognise within Group III. Among the many species previously included in *Leucopogon* that have this same basic floral configuration, *S. subulata* can be distinguished by the following character combination: strongly recurved to revolute leaf margins, deeply grooved and hairy abaxial leaf surfaces and internal corolla tubes that are hairy below the lobes for much of their length.

Aside from the different style and anther presentation seen in *S. subulata*, species from the *S. intertexta* group have a very similar general morphology. Differences in vegetative indumentum, leaf shape, corolla tube length and hair distribution are used to demarcate species.

Distribution. Collectively the species of Group III are distributed disjunctly from the south coast of Western Australia to well north of Southern Cross and east to the Great Victoria Desert. The three species with long-exserted anthers and styles have widely allopatric distributions mostly centred on different bioregions. While *Styphelia intertexta* is restricted to within about 100 kilometres of the south coast, *S. deserticola* and *S. saxicola* share an eremaean distribution. Very few epacrids have penetrated as far into the interior of Western Australia as these species.

Styphelia subulata is the most widespread in the group with a distribution that encompasses four bioregions. It is sympatric with *S. intertexta* in the south of its range and with *S. saxicola* in the north.

Styphelia deserticola Hislop, *sp. nov.*

Holotypus: Great Victoria Desert, Western Australia [precise locality withheld for conservation reasons], 21 July 2010, *N. Murdock NM 44* (PERTH08214921).

Styphelia sp. Great Victoria Desert (*N. Murdock 44*) Western Australian Herbarium, *FloraBase* http://florabase.dpaw.wa.gov.au [accessed: 6 Mar. 2020].

Styphelia intertexta auct. non. A.S.George, Paczk. & A.R.Chapm., *W. Austral. Fl. Descr. Cat.* 242 (2000), *p.p.* (as to reference to Great Victoria Desert bioregion).

Erect *shrubs* to c. 90 cm high and 90 cm wide; rootstock unknown. Young *branchlets* with a sparse to moderately dense indumentum of patent to shallowly retrorse hairs, to c. 0.15 mm long. *Leaves* strongly antrorse to strongly retrorse; apex long-mucronate, pungent, the mucro 0.4–1.0 mm long; base mostly cuneate, or occasionally rounded; petiole 0.3–0.6 mm long; lamina narrowly ovate, narrowly triangular or linear, 5–9.5 mm long, 1.0–2.1 mm wide, adaxially convex with strongly recurved

Key to species

1. Anthers partially included in the corolla tube, or if occasionally exserted, then barely so; style included in the corolla tube; corolla lobes to 2.5 mm long, always shorter than the tube, recurved to revolute, occasionally partially coiled abaxially (Quairading–Koolyanobbing–Stirling Range–Israelite Bay) . . . . . ***S. subulata***

1: Anthers long-exserted from corolla tube; style long-exserted from the corolla tube; corolla lobes at least 3 mm long, usually longer than the tube (occasionally shorter), always revolute and coiled abaxially

2. Corolla tube 1.2–2.0 mm long, always shorter than the sepals; sepals 2.0–2.6 mm long; internal surface of corolla tube with hairs restricted to a narrow ring immediately below the lobes, i.e. in the distal ¼ (Great Victoria Desert) . . . . . ***S. deserticola***

2: Corolla tube 2.2–5.0 mm long, usually longer than the sepals (occasionally shorter in *S. intertexta*); the sepals 2.5–3.6 mm long; internal surface of corolla tube hairy in the distal ⅓–¾

3. Leaf base cordate or rounded, rarely cuneate; leaf lamina narrowly triangular, narrowly ovate or occasionally ± linear, longest leaves to 9 mm long but usually less; leaf mucros straight or deflexed, the longest to 1.2 mm; abaxial leaf hairs slightly antrorse to slightly retrorse, 0.05–0.1 mm long; branchlet indumentum usually moderately dense with spreading hairs, 0.1–0.3 mm long, less often sparse and to 0.05 mm (Ongerup–Thomas River–Frank Hann National Park) . . . . . ***S. intertexta***

3: Leaf base cuneate or attenuate; leaf lamina linear, very narrowly elliptic or very narrowly triangular, longest leaves at least 9 mm, usually longer; leaf mucros straight or inflexed, the longest to 1.9 mm; abaxial leaf hairs usually markedly antrorse throughout, but at least in the upper half, to 0.05 mm long; branchlet indumentum always sparse, to 0.05 mm long (Bullfinch–Bullabulling–Diemals) . . . . . ***S. saxicola***

margins, longitudinal axis gently incurved to gently recurved, the mucro slightly inflexed to slightly deflexed; surfaces strongly discolorous; adaxial surface shiny, ± rugose, longitudinal grooves lacking or indistinct, mostly glabrous but often with a few hairs towards the base and sometimes also the apex; abaxial surface much paler, usually partially concealed by recurved leaf margins, with 7–9 raised veins and deep grooves between, hairy in the grooves, ± glabrous on the exposed vein surfaces, the groove hairs spreading, throughout, or distinctly antrorse towards the apex; margins glabrous or sparsely ciliolate with coarse antrorse hairs. *Inflorescence* axillary; axis 1.1–2.0 mm long, 2–3 (4)-flowered, hairy throughout. *Fertile bracts* depressed-ovate, 0.5–0.7 mm long, 0.7–1.0 mm wide, subtended by 2 pairs of opposite and decussate sterile bracts, or occasionally a single pair only. *Bracteoles* depressed ovate, 0.9–1.2 mm long, 1.0–1.4 mm wide, obtuse with a very short sub-terminal mucro; abaxial surface not striate, keeled, glabrous or with a few short hairs about the keel, straw-coloured to pale brown; margins minutely ciliolate. *Sepals* ovate or narrowly ovate, 2.0–2.6 mm long, 1.1–1.5 mm wide, obtuse; abaxial surface glabrous, pale greenish to straw-coloured, venation usually not conspicuous, but occasionally quite distinct; adaxial surface with a sparse patch of hairs towards the base, otherwise glabrous; margins ciliolate, the hairs to c. 0.1 mm long at the apex. *Corolla tube* white or pale cream, obovoid or ellipsoid, shorter than the sepals, 1.2–2.0 mm long, 1.3–1.7 mm wide, glabrous externally, internal surface with hairs restricted to a narrow ring immediately below the lobes, i.e. in the distal ¼. *Corolla lobes* white or pale cream, sometimes tinged pink towards the apex in bud, much longer than the tube, 3.2–4.5 mm long, 0.6–1.0 mm wide at base, spreading from the base, revolute and coiled abaxially; external surface glabrous, internal surface with a dense indumentum of twisted and ornamented hairs. *Filaments* terete, glabrous, 2.5–4.0 mm long, attached to the anther ½–⅔ above the base, adnate to the tube just below sinuses. *Anthers* long-exserted from the tube, 1.5–2.2 mm long, apex shallowly emarginate. *Nectary* annular, 0.3–0.5 mm long, deeply lobed and longitudinally grooved below sinuses. *Ovary* mid to dark green, ovoid or ellipsoid, 0.7–1.0 mm long, 0.6–0.7 mm wide, glabrous, 5-locular. *Style* glabrous and smooth throughout, 4.2–6.0 mm long, well-differentiated from the ovary apex, long-exserted from the corolla tube; stigma slightly expanded. *Fruit* ellipsoid or broadly ellipsoid, 4.4–6.0 mm long, 3.3–4.7 mm wide, much longer than the calyx, circular in section, apex rounded; surface glabrous, rugose (mesocarp well-developed); style usually shed, in part or whole, at maturity. **Fig. 1.**

Diagnostic characters. Distinguished from other species in Group III with long-exserted styles and anthers by the consistently short corolla tube (always shorter than the sepals) and in having the internal

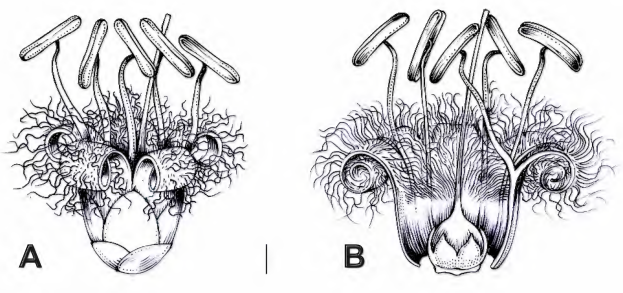

Fig. 1. *Styphelia deserticola*. A Flower, external view; **B** flower, internal view. Scale bar = 1 mm. — *G. Cockerton s.n.* Drawings by Hung Ky Nguyen.

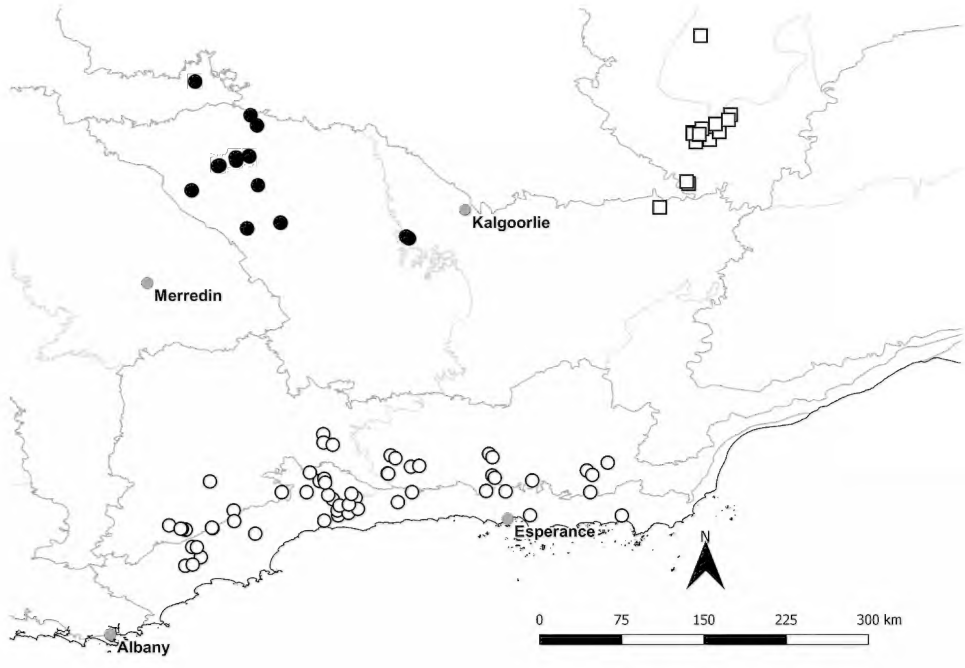

Fig. 2. Distribution of *Styphelia deserticola* (open squares), *S. intertexta* (open circles) and *S. saxicola* (black circles) in Western Australia.

corolla tube hairs restricted to a narrow distal band (in the distal ¼ or less) immediately below the lobe bases.

Distribution and habitat. Distributed in the western Great Victoria Desert bioregion and the adjacent far east of the Coolgardie bioregion (Fig. 2). Occurs on plains or dunes in yellow sandy soils in the understorey of open eucalypt woodland or shrubland. Commonly associated species include *Eucalyptus gongylocarpa*, *E. youngiana*, *Allocasuarina acutivalvis*, *Calothamnus gilesii*, *Leptospermum fastigiatum*, *Triodia desertorum* and *Lepidobolus deserti*.

Phenology. Flowering collections have been made between March and August and collections with mature fruit between August and November. Large fluctuations in annual rainfall are the norm in the desert country where this species occurs and this will presumably have a significant bearing on the timing of phenological events.

Etymology. From the Latin *desertum* (desert) and *-cola* (inhabitant), a reference to the desert region where the species occurs.

Conservation status. Currently listed by Smith & Jones (2018) as Priority Two under Conservation Codes for Western Australian Flora under the name *Styphelia* sp. Great Victoria Desert (*N. Murdock 44*).

Affinities. *Styphelia deserticola* is the only species in Group III not to have been placed in the phylogenetic tree of Puente-Lelièvre *et al.* (2016). The morphological case for its inclusion however, is very strong as it shares all critical foliar, floral and fruiting characters with *S. intertexta* and *S. saxicola*.

The species can be distinguished from *Styphelia intertexta* and *S. saxicola* by its short corolla tubes (1.2–2 mm long) that are always shorter than the sepals, and internal corolla tube hairs that are restricted to a narrow distal band below the lobe bases. By comparison, *S. intertexta* and *S. saxicola* have longer tubes (2.2–5 mm long) that are usually longer than the sepals, and more widely distributed hairs in the internal corolla tube (i.e. across the distal ⅓ to more than ¾).

While *Styphelia intertexta* occasionally has the sepals longer than the corolla tubes, specimens with this morphology can be further distinguished from *S. deserticola* by their generally longer sepals (at least 2.6 mm long *cf.* 2.0–2.6 mm) and by a difference in their abaxial leaf surfaces. In *S. intertexta* the exposed vein surfaces are hairy whereas in *S. deserticola* they are glabrous, or almost so.

In addition to the characters cited above, *Styphelia deserticola* differs from *S. saxicola* in almost always having shorter leaf mucros (0.4–1.0 mm long *cf.* 0.8–1.9 mm), a noticeably longer branchlet indumentum (to 0.15 mm long *cf.* to 0.05 mm) and generally shorter leaves. The two species also occupy different habitats with *S. deserticola* occurring on sandplains and dunes and *S. saxicola* restricted to elevated, rocky sites. The closest known populations of these two species are about 280 km apart.

During the preparation of his description of *Styphelia intertexta*, Alex George (1967) saw one collection each of the species described here as *S. deserticola* (i.e. *D.E. Goodall 2946*) and *S. saxicola* (i.e. *J.S. Beard 3348*). While he assigned both to his new species he did note some of the differences in indumentum and flower size, that have been partly employed by the current author to distinguish between species in this tight-knit group.

Other specimens examined [precise localities withheld for conservation reasons]

WESTERN AUSTRALIA: [Sep.] 1967, *P. Boswell C19* (PERTH); 21 Mar. 2017, *G. Cockerton s.n.* (PERTH); 8 Apr. 2014, *L. Cockram LAC 23* (PERTH); 2 Nov. 2010, *M. Gannaway 22* (PERTH); 2 July 1966, *D.W. Goodall 2946* (PERTH); 2 Nov. 2010, *N. Murdock 55* (PERTH); 3 Nov. 2010, *N. Murdock 57* (PERTH); 10 Apr. 2014, *N. Murdock NM 59* (PERTH); 10 Apr. 2014, *N. Murdock 74* (PERTH); 9 Aug. 2014, *N. Murdock NM 115* (PERTH); 12 Aug. 2014, *N. Murdock NM 136* (PERTH); 13 Aug. 2014, *N. Murdock NM 144* (PERTH); 14 Aug. 2014, *N. Murdock NM 145* (PERTH); May 2009, *B. Sadlo s.n.* (PERTH).

Styphelia intertexta A.S.George

J. Roy. Soc. Western Australia 50: 101, fig. 4D–I (1967). — **Holotype:** 9 miles N. of Ravensthorpe [Western Australia], 25 May 1963, *A.S. George 4431* (PERTH01597892). **Isotypes:** K000848149, MEL707612.

Erect *shrubs* to c. 1.5 m high and 1.2 m wide, but usually less than 1 m, with a fire-sensitive rootstock. Young *branchlets* usually with a moderately dense to dense indumentum of ± patent hairs, 0.1–0.3 mm long, or occasionally the indumentum ± absent or very sparse and <0.05 mm long. *Leaves* shallowly antrorse to strongly retrorse; apex long-mucronate, pungent, the mucro 0.7–1.2 mm long; base cordate or rounded, rarely cuneate; petiole often obscured by lamina, 0.3–0.5 mm long; lamina usually narrowly triangular or narrowly ovate, or occasionally ± linear, 4–9 mm long, 1.3–2.7 mm wide, adaxially convex with strongly recurved to revolute margins, longitudinal axis ± straight, the mucro straight or deflexed; surfaces strongly discolorous; adaxial surface shiny, ± rugose, often markedly so, longitudinal grooves lacking or very indistinct, mostly glabrous but often with a few hairs towards the base and sometimes also the apex; abaxial surface much paler, usually partially, and sometimes completely concealed by recurved leaf margins, with 7–9 raised veins and deep grooves between, densely hairy in the grooves, more sparsely hairy, and with shorter hairs, on the exposed vein surfaces, the groove hairs spreading (from slightly antrorse to slightly retrorse) throughout; margins glabrous or sparsely ciliolate with coarse antrorse hairs. *Inflorescence* axillary; axis 1.7–2.8 mm long, 2–3 (4)-flowered, sparsely hairy in lower portion, more densely hairy above the first fertile node. *Fertile bracts* broadly ovate, broadly elliptic to ± orbicular, 1.0–1.4 mm long, 0.8–1.3 mm wide, subtended by 2 pairs of opposite and decussate sterile bracts. *Bracteoles* depressed-ovate, broadly ovate or ± orbicular, 1.1–1.6 mm long, 1.0–1.6 mm wide, obtuse with a very short sub-terminal mucro; abaxial surface not striate, keeled, glabrous, straw-coloured to pale brown; margins minutely ciliolate. *Sepals* narrowly ovate, 2.6–3.6 mm long, 1.2–1.6 mm wide, obtuse; abaxial surface glabrous, or very occasionally with a very short appressed indumentum, straw-coloured or pale brown, venation inconspicuous; adaxial surface with a sparse patch of hairs towards the base, otherwise glabrous; margins ciliolate, the hairs to c. 0.1 mm long at the apex. *Corolla tube* white or pale cream, cylindrical, or narrowly obovoid, a little shorter than, to distinctly longer than the sepals, 2.2–4.0 (5.0) mm long, 1.3–1.7 mm wide, glabrous externally, internal surface hairy in the distal ⅓–⅔. *Corolla lobes* white or pale cream, usually much longer than, but occasionally ± equal to the tube, 3.6–5.2 mm long, 0.7–1.0 (–1.2) mm wide at base, spreading from the base, revolute and coiled abaxially; external surface glabrous, internal surface with a dense indumentum of twisted and ornamented hairs. *Filaments* terete, glabrous, 2.5–3.8 mm long, attached to anther ½–⅔ above the base, adnate to tube just below sinuses. *Anthers* long-exserted from the tube, 1.2–2.0 mm long, apex shallowly emarginate. *Nectary* annular, 0.4–0.5 mm long, glabrous, shallowly lobed or ± truncate. *Ovary* mid to dark green, ellipsoid or ovoid, 0.7–1.0 mm long, 0.6–0.7 mm wide, glabrous, 5-locular. *Style* glabrous and smooth throughout, or hairy towards the base, 4.8–7.6 (–8.3) mm long, well-differentiated from ovary apex, long-exserted from the corolla tube; stigma slightly expanded. *Fruit* ellipsoid, 3.5–5.0 mm long, 2.5–3.3 mm wide, much longer than the calyx, circular in section, apex rounded; surface glabrous, rugose (mesocarp well developed); style usually shed, in whole or part, at maturity. **Fig. 3.**

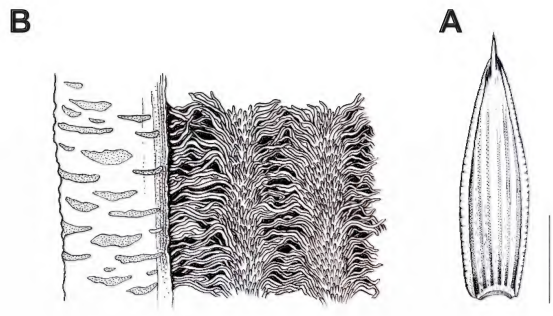

Fig. 3. *Styphelia intertexta*. A Leaf, abaxial surface; **B** abaxial surface detail. Scale bar = 2 mm (A). — *M. Hislop 3706*. Drawings by Hung Ky Nguyen.

Diagnostic characters. Distinguished from other species in Group III with long-exserted styles and anthers by the cordate or rounded (rarely cuneate) leaf bases, internal corolla tubes with hairs in the distal ⅓–⅔, relatively long (0.05–0.1 mm), spreading abaxial leaf hairs and usually a moderately dense branchlet indumentum, the hairs 0.1–0.3 mm long.

Distribution and habitat. Widely distributed in the Mallee and Esperance Plains bioregions from near Ongerup in the west to the Thomas River in the east and as far north as Frank Hann National Park (Fig. 2). Most commonly collected from mallee woodland in flat country, very occasionally from lateritic uplands. Apparently tolerates a variety of soil types although herbarium records suggest a preference for sand or light loam soils, at least at the surface.

Phenology. Flowering is mostly between March and July with a peak between April and June. Specimens with mature fruit have been collected in September and October, but fruit is likely to be present at least until December.

Conservation status. Widespread and locally common. No conservation code is recommended here.

Affinities. *Styphelia intertexta* is a variable species in regard to branchlet indumentum, rugosity of adaxial leaf surfaces, corolla tube length relative to both sepal length and corolla lobe length, and most interestingly in presence/absence of hairs on lower half of the style.

The branchlet indumentum is of two types: either moderately dense to dense and 0.1–0.3 mm long or very sparse and up to about 0.05 mm long (the branchlets sometimes more or less glabrous). The latter is the less common condition and occurs only in the west and north-west of the species' range. However, this indumentum difference does not appear to correlate with any other morphological character difference.

All but one of the examined collections had corolla tubes up to 4 mm long. Mostly these are longer than the sepals (by up to 1.5 mm) but occasionally shorter. The flowers of *G.F. Craig & B. Haberley 2732* however, are significantly larger with tubes 5 mm long and 2 mm longer than the sepals. The style length of 8.3 mm long is also appreciably longer than the maximum of 7.6 mm that was otherwise recorded for the species. No correlating qualitative differences were observed however, and at this stage it is considered here to represent only a morphological extreme within the species and unlikely to be of taxonomic significance.

The presence of hairs on the style is an uncommon feature in western *Styphelia*. Elsewhere in Group III it only occurs very occasionally in *S. subulata*. That it should be an inconsistent character at the species level is of interest in itself. Only two other western *Styphelia* have well-developed stylar hairs (although many have scabrous styles), the highly anomalous *S. kingiana* F.Muell. and *S. rectiloba* Hislop. In both of these species the style hairs are a fixed character.

Notes. A collection from the remote Jilbadji Nature Reserve, south-east of Marvel Loch, is significantly anomalous and may represent a distinct taxon. While *P.G. Armstrong PA 13/044* is morphologically most similar to *S. intertexta*, it differs from all other collections of the species at PERTH in the following ways: shorter leaves, all <4 mm long, with short mucros to 0.5 mm long, longer hairs on the leaf undersurfaces and sparse, coarse antrorse hairs on the upper leaf surfaces; smaller flowers with sepals to 1.8 mm long and corolla lobes c. 3 mm long. The area of collection is well to the north of the species' known distribution. More material of this entity needs to be seen before its status can be properly assessed.

Selected specimens examined

WESTERN AUSTRALIA: Lake Tay Rd, 600 m N of Cascades Rd, 21 Apr. 2013, *W.R. Archer 21041313* (PERTH); Carney Rd [SE of Ongerup], 21 Feb. 2011, *G. Byrne 4042* (DNA, PERTH); 12 km NW of Parmango Rd on Clyde Rd, NW of Clyde Hill, 19 May 1993, *G.F. Craig & B. Haberley 2732* (NSW, PERTH); Wittenoom Hills [E of Scaddan], 9 June 1972, *T. Daniells s.n.* (PERTH); 27 miles [approx. 43.4 km] W of Ravensthorpe & 20 miles [approx. 32.2 km] N of main road, 30 Oct. 1965, *A.S. George 7073* (CANB, PERTH); near Twertup Creek, Fitzgerald River National Park, 11 July 1970, *A.S. George 9908* (PERTH); Muntz Nature Reserve [NE of Condingup], 0.8 km NE along Muntz Rd from intersection with Bebenorin Rd, 3 Sep. 2001, *E. Hickman & S. Gilfillan EJH 1204* (PERTH); Kendall Rd, 5.8 km W of Norwood Rd, E of Scaddan, 20 May 2002, *M. Hislop & F. Hort MH 2648* (PERTH); Cascades Rd, 80.9 km W of West Point Rd, 23 May 2004, *M. Hislop & F. Hort MH 3230* (PERTH); west side of Ravensthorpe–Lake King Rd, c. 3 km N of Bridge Rd, 25 June 2007, *M. Hislop 3706* (NSW, PERTH); remnant vegetation, Jerramungup townsite, adjacent Caravan Park, 1 Apr. 2012, *M. Hislop 4182* (CANB, MEL, PERTH); 11 km SSE of Mt Gibbs, Frank Hann National Park, c. 33 km ENE of Lake King, 22 July 1979, *K.R. Newbey 5441* (PERTH); between Munglinup and Ravensthorpe, near branch of Oldfield River, c. 75 km E of Ravensthorpe, 20 July 1982, *J.M. Powell 1886* (NSW, PERTH); breakaway laterite area on Norman Rd, 25 km NNW of Boxwood Hill, 3 Aug. 1986, *J.M. Powell 2428* (HO, K, NSW, PERTH); Ongerup–Needilup Rd, 1 km W of Gleeson Rd, 1 Sep. 1986, *J.M. Powell 2798* (CANB, NSW, PERTH); 27.2 km E of Ravensthorpe towards Esperance on South Coast Hwy, 4 Sep. 1986, *J.M. Powell 2862* (HO, K, NSW, PERTH); lot 4, Blue Vista, 15 km N of Hopetoun, 23 Apr. 1998, *H. Taylor 32* (PERTH); Lake Magenta Nature Reserve, 3 May 1999, *S. Walsh 71* (PERTH).

Styphelia saxicola Hislop, *sp. nov.*

Holotypus: east of Bullfinch, Western Australia [precise locality withheld for conservation reasons], 16 Apr. 2006, *M. Hislop 3574* (PERTH07520204). **Isotypi:** CANB, MEL, NSW.

Styphelia sp. Bullfinch (*M. Hislop 3574*) Western Australian Herbarium, *FloraBase* http://florabase.dpaw.wa.gov.au [accessed: 6 Mar. 2020].

Styphelia intertexta auct. non. A.S.George: W.E.Blackall & B.J.Grieve, *How to know W. Austral. Wilfl.* IIIB: 303 (1981), *p.p.* (as to reference to Coolgardie District, Bullabulling); Paczk. & A.R.Chapm., *W. Austral. Fl. Descr. Cat.* 242 (2000), *p.p.* (as to reference to Coolgardie bioregion).

Erect *shrubs* to c. 1.0 m high and 1.0 m wide, with a fire-sensitive rootstock. Young *branchlets* with a sparse indumentum of very short hairs, to 0.05 mm long, or ± glabrous. *Leaves* strongly antrorse to shallowly retrorse; apex long-mucronate, pungent, the mucro 0.8–1.9 mm long; base cuneate to attenuate; petiole 0.3–0.6 mm long; lamina linear, very narrowly elliptic or very narrowly triangular (very rarely narrowly ovate), 6–14 mm long, 0.9–1.5 (–2.0) mm wide, adaxially convex with recurved

to revolute margins, longitudinal axis gently incurved to gently recurved, the mucro straight or ± inflexed; surfaces discolorous; adaxial surface shiny, usually ± rugose, 1–3 indistinct longitudinal grooves usually apparent, sometimes completely lacking, glabrous or with a few hairs towards the base and apex; abaxial surface paler, usually partially, and sometimes completely concealed by recurved leaf margins, with 5–7 raised veins and deep grooves between, hairy in the grooves, more sparsely so on the exposed vein surfaces or ± glabrous, the groove hairs usually distinctly antrorse throughout, or at least in the upper half; margins glabrous or sparsely ciliolate with coarse antrorse hairs. *Inflorescence* axillary; axis 1.5–2.4 mm long, 2–3-flowered, hairy throughout. *Fertile bracts* broadly ovate to ± orbicular, 0.7–1.0 mm long, 0.7–0.9 mm wide, subtended by 2 pairs of opposite and decussate sterile bracts, sometimes with a fifth bract inserted above the others. *Bracteoles* depressed-ovate, broadly ovate or ± orbicular, 1.0–1.3 mm long, 1.2–1.5 mm wide, obtuse with a very short sub-terminal mucro; abaxial surface not striate, keeled, glabrous or shortly hairy in the upper half and about the keel, straw-coloured to pale brown; margins ciliolate. *Sepals* narrowly ovate, 2.5–3.0 mm long, 1.2–1.5 mm wide, obtuse; abaxial surface glabrous, or shortly hairy towards the apex, straw-coloured to pale brown, sometimes flushed pink distally, venation inconspicuous; adaxial surface with a sparse patch of hairs towards the base, otherwise glabrous; margins ciliolate, the hairs to c. 0.2 mm long at the apex. *Corolla tube* white or pale cream, cylindrical, longer than the sepals, (2.4–) 3.3–4.7 mm long, 1.5–2.0 mm wide, glabrous externally, internal surface hairy in the distal ½–¾. *Corolla lobes* white or pale cream, usually tinged pink towards the apex in bud, longer than, or occasionally shorter than, the tube, 3.0–4.6 mm long, 0.7–1.0 mm wide at base, spreading from the base, revolute and coiled abaxially; external surface glabrous, internal surface with a dense indumentum of twisted and ornamented hairs. *Filaments* terete, glabrous, 2.5–4.0 mm long, attached to anther ½–⅔ above the base, adnate to tube just below the sinuses. *Anthers* long-exserted from the tube, 1.3–2.3 mm long, apex emarginate. *Nectary* annular, 0.4–0.6 mm long, glabrous, variably lobed and often longitudinally grooved below the sinuses. *Ovary* mid green, ellipsoid or occasionally ± globose, 0.7–1.2 mm long, 0.5–0.8 mm wide, glabrous, 5-locular. *Style* glabrous and smooth throughout, 3.5–8.5 mm long, well-differentiated from ovary apex, long-exserted from corolla tube; stigma slightly expanded. *Fruit* ellipsoid or narrowly ellipsoid, 3.6–4.5 mm long, 2.2–2.8 mm wide, much longer than the calyx, circular in section, apex rounded; surface glabrous, rugose (mesocarp well developed); style shed in whole or part, at maturity. **Figs 4, 5.**

Diagnostic characters. Distinguished from other species in Group III with long-exserted styles and anthers by the cuneate to attenuate leaf bases, internal corolla tubes with hairs in the distal ½–¾, short (to 0.05 mm long), antrorse, abaxial leaf hairs, relatively long and often inflexed leaf mucros and a consistently sparse branchlet indumentum, the hairs to 0.05 mm long.

Distribution and habitat. Mostly occurs in the Coolgardie bioregion with one record from the adjacent Yalgoo; from Bullfinch and Bullabulling in the south northwards to the Diemals area (Fig. 2). All records are from shallow soils on rocky sites with a lateritic, granitic or ironstone geology. Associated vegetation is usually open shrubland.

Phenology. Flowering specimens have been collected between April and September and collections with mature fruit have been made in September and November. It is likely that the apparently extended flowering season is an artefact of the unreliable rainfall pattern across the species' range. It can be anticipated that the species will flower during the period April to July under average seasonal conditions, but if the rains fail during late autumn and early winter it apparently has the capacity to come into flower later, soil moisture allowing.

Etymology. From the Latin *saxum* (rock, stone) and *-cola* (inhabitant), a reference to the rocky habitats to which the species is apparently restricted.

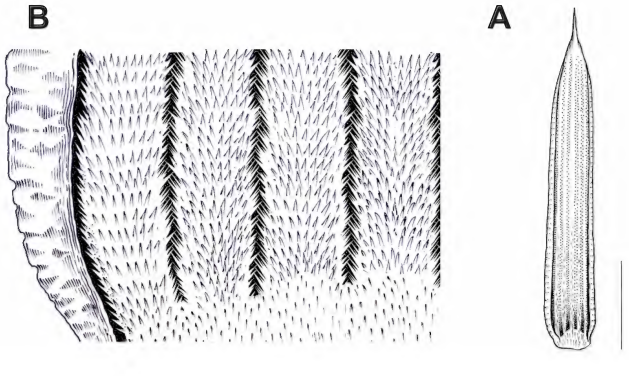

Fig. 4. *Styphelia saxicola.* **A** Leaf, abaxial surface; **B** abaxial surface detail. Scale bar = 2 mm (A). — *A.S. George 14318*. Drawings by Hung Ky Nguyen.

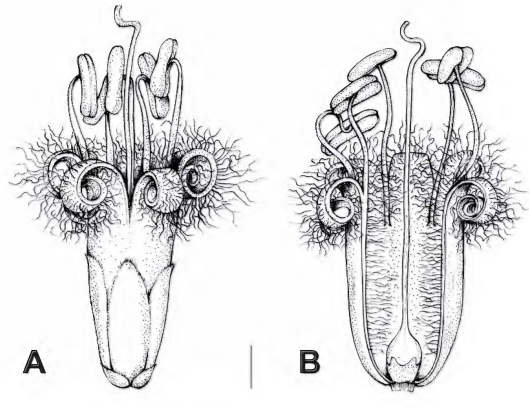

Fig. 5. *Styphelia saxicola.* **A** Flower, external view; **B** flower, internal view. Scale bar = 1 mm. — *M. Hislop 3574*. Drawings by Hung Ky Nguyen.

Conservation status. Currently listed by Smith & Jones (2018) as Priority Three under Conservation Codes for Western Australian Flora under the name *Styphelia* sp. Bullfinch (*M. Hislop 3574*).

Affinities. In the phylogenetic tree of Puente-Lelièvre *et al.* (2016), *Styphelia saxicola* (as *Styphelia* sp. Bullfinch) is placed as sister to the species-pair *S. intertexta* and *S. subulata*.

Because of the shared characters of long-exserted anthers and style, *Styphelia saxicola* is only likely to be confused with *S. intertexta* and *S. deserticola*. From *S. intertexta* it is distinguished largely on the basis of differences in foliar morphology. There appear to be no reliable differences in flowers or fruit between the two species, although while *S. intertexta* frequently has stylar hairs these are always absent in *S. saxicola*.

Compared to that of *Styphelia intertexta* the abaxial leaf indumentum of *S. saxicola* differs in its orientation (hairs usually markedly antrorse throughout, but at least in the upper half, *cf.* hairs spreading, from slightly antrorse to slightly retrorse, in *S. intertexta*) and in being noticeably less dense. The abaxial leaf hairs also tend to be shorter in *S. saxicola* (longer hairs to 0.05 mm long *cf.* 0.05–0.1 mm in *S. intertexta*). The leaf base of *S. saxicola* is cuneate to attenuate whereas it is either cordate or rounded in *S. intertexta*, rarely cuneate.

There are also differences in leaf length and shape, with the leaves of *Styphelia saxicola* being longer (the longest leaves on any specimen being at least 9 mm long, usually more than 10 mm *cf.* rarely as long as 9 mm in *S. intertexta*) and generally narrower (either linear, very narrowly elliptic or very narrowly triangular, *cf.* narrowly triangular, narrowly ovate or occasionally more or less linear). The leaf mucros of *S. saxicola* are usually noticeably longer than those of *S. intertexta* (the longest to 1.9 mm *cf.* to 1.2 mm) and often inflexed, whereas in *S. intertexta* if the mucros are not straight they are deflexed.

There is frequently another useful vegetative difference between the two species. The most common type of branchlet indumentum in *Styphelia intertexta* consists of rather dense, spreading hairs, 0.1–0.3 mm long. By comparison that of *S. saxicola* is sparse, with the hairs to about 0.05 mm long. However, this difference is only partial, as *S. intertexta* has a similar short, sparse indumentum in the west and north-western parts of that species' range.

There is a major disjunction between the distributions of *Styphelia saxicola* and *S. intertexta* with the former occurring in the Coolgardie and Yalgoo bioregions north of Great Eastern Highway and *S. intertexta* within about 100 kilometres of the south coast in the Mallee and Esperance Plains bioregions.

It is noteworthy that although the foliar differences, as described above, allow a complete differentiation between *Styphelia saxicola* and *S. intertexta*, this is not the case between *S. saxicola* and *S. subulata*. The variability evident in the latter species encompasses most of the foliar variation used to distinguish *S. saxicola* from *S. intertexta*. Non-flowering material of *S. saxicola* is therefore very difficult to distinguish from *S. subulata* in the absence of accompanying habitat information. The only vegetative character likely to be useful is the leaf mucros: straight to inflexed in *S. saxicola*, straight to deflexed in *S. subulata*. These two species are known to occur within about thirty kilometres of each other in the Bullfinch area, but with *S. subulata* growing on flats adjacent to salt lakes, and *S. saxicola* restricted to rocky uplands, they are unlikely to be confused.

The differences between *Styphelia saxicola* and *S. deserticola* are discussed above under the latter species.

Other specimens examined [precise localities withheld for conservation reasons]

WESTERN AUSTRALIA: 25 May 1964, *J.S. Beard 3348* (PERTH); 13 May 2004, *G. Cockerton & S. McNee LCH 12225* (PERTH); 16 June 2006, *G. Cockerton & S. McNee LCH 12226* (MEL, NSW, PERTH); 1 Sep. 2013, *D. Coultas & S. Coultas 140–Opp01* (PERTH); 4 July 1976, *A.S. George 14318* (NSW, PERTH); 23 Sep. 2012, *J. Gilovitz CG 274* (PERTH); 7 Nov. 2000, *M. Griffiths 220-MG 008* (PERTH); 17 June 2006, *S. McNee LCS 13652* (PERTH); 27 Aug. 2006, *S. McNee & B. Eckermann LCS 13653* (PERTH); 22 Sep. 1982, *K.R. Newbey 9575* (PERTH); 18 Nov. 1993, *H. Pringle 30155* (PERTH); 28 July 2010, *S. Reiffer SRE 222* (PERTH); 28 July 2010, *S. Reiffer SRE 226* (CANB, PERTH); 28 July 2010, *S. Reiffer SRE 236* (PERTH); 8 Sep. 2010, *S. Reiffer SRE 294* (PERTH); 11 Sep. 2013, *B. Sadlo BS 400* (PERTH).

Styphelia subulata (F.Muell.) Hislop, Crayn & Puente-Lel.

Austral. Syst. Bot. 33: 152 (2020). — *Leucopogon subulatus* F.Muell., *Fragm.* 4: 103 (1864); *Styphelia subulifolia* F.Muell., *Fragm.* 6: 33 (1867), *nom. illeg.* — **Type citation:** "In vallibus arenosis partem orientalem versus sinus marini Great Australian Bight; e.g. ad Eagle Hawk Camp [south coast of Western Australia], Maxw.". **Syntypes:** "Sandy hollows between Eagle Hawk camp & the Bank / Plants 2 ft", *s.dat., G. Maxwell s.n.* (MEL88986); "among Sandy valeys [sic] between Eagle Hawk Camp & the Bank / Pts 2 ft", *s.dat., G. Maxwell s.n.* (MEL88988).

Leucopogon sp. Kau Rock (*M.A. Burgman 1126*) Western Australian Herbarium, *FloraBase* http://florabase.dpaw.wa.gov.au [accessed 6 Mar. 2020].

Erect *shrubs* to c. 1.0 m high and 1.0 m wide, with a fire-sensitive rootstock. Young *branchlets* usually with a sparse indumentum of very short hairs, <0.5 mm long, or ± glabrous, less often with a moderately dense to dense indumentum of ± patent hairs, 0.1–0.3 mm long. *Leaves* mostly shallowly antrorse to shallowly retrorse; apex long-mucronate, pungent, the mucro 0.7–1.4 mm long; base cordate, rounded or cuneate; petiole 0.2–0.6 mm long;

lamina narrowly triangular, narrowly ovate, or ± linear, 5–12 mm long, 1.2–1.8 mm wide, adaxially convex with strongly recurved to revolute margins, longitudinal axis straight or gently recurved, the mucro straight or ± deflexed; surfaces strongly discolorous; adaxial surface shiny, usually rugose, occasionally almost smooth, 1–3 longitudinal grooves usually apparent, but occasionally absent, most of surface glabrous but often with a few hairs towards the base and the apex; abaxial surface much paler, usually partially, and sometimes completely concealed by recurved leaf margins, with 7–9 raised veins and deep grooves between, hairy in the grooves, usually more sparsely so on the exposed vein surfaces (refer comment under Affinities heading for *S. saxicola* in regard to this character); margins glabrous or sparsely ciliolate with coarse antrorse hairs. *Inflorescence* axillary; axis 1.7–2.5 mm long, 2–3-flowered, usually hairy throughout. *Fertile bracts* broadly ovate to ± orbicular, 0.7–1.0 mm long, 0.6–1.0 mm wide, subtended by 2 pairs of opposite and decussate sterile bracts, sometimes with a fifth bract inserted above the others. *Bracteoles* depressed-ovate, broadly ovate or ± orbicular, 0.9–1.4 mm long, 1.0–1.5 mm wide, obtuse with a very short, sub-terminal mucro; abaxial surface not striate, keeled, glabrous, straw-coloured to pale brown; margins minutely ciliolate. *Sepals* ovate to narrowly ovate, 2.1–3.0 mm long, 1.2–1.6 mm wide, obtuse; abaxial surface glabrous, straw-coloured or pale brown, venation inconspicuous; adaxial surface with a discrete patch of hairs towards the base, otherwise glabrous; margins ciliolate, the hairs to c. 0.2 mm long at the apex. *Corolla tube* white or pale cream, cylindrical, longer than the sepals, 2.5–3.7 mm long, 1.4–2.0 mm wide, glabrous externally, internal surface hairy, except at the base. *Corolla lobes* white or pale cream, shorter than the tube, 1.8–2.5 mm long, 0.8–1.2 mm wide at base, spreading from close to the base, and recurved to revolute, occasionally partially coiled abaxially; external surface glabrous, internal surface with a dense indumentum of twisted and ornamented hairs. *Filaments* terete, glabrous, 0.5–0.7 (–0.9) mm long, attached to anther ½–⅔ above the base, adnate to tube just below sinuses. *Anthers* partially exserted from tube by ¾ of their length, to fully, but barely exserted, 0.8–1.5 mm long, apex shallowly emarginate. *Nectary* annular, 0.3–0.5 mm long, glabrous, shallowly lobed and usually longitudinally grooved below the sinuses. *Ovary* mid green, ovoid to ellipsoid, 0.7–1.2 mm long, 0.6–0.8 mm wide, glabrous, 5-locular. *Style* glabrous and smooth throughout, or very occasionally hairy in the lower half, 1.5–2.5 mm long, abruptly differentiated from ovary apex, included within the corolla tube with the stigma usually presented at the throat or below; stigma slightly expanded. *Fruit* ± globose to ellipsoid, 3.0–3.7 mm long, 2.7–3.5 mm wide, much longer than calyx, circular in section, apex rounded; surface glabrous, rugose (mesocarp well-developed); style usually shed at maturity. **Fig. 6.**

Diagnostic characters. Distinguished from the other species in Group III in being the only one with an included style and usually partially included, or occasionally very shortly exserted, anthers.

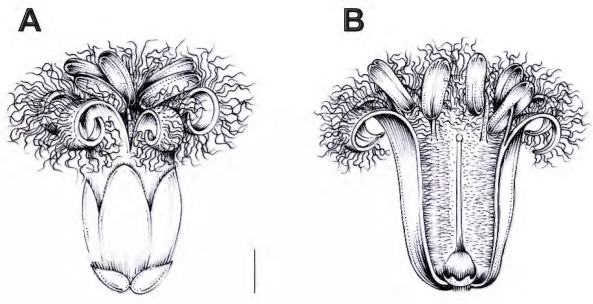

Fig. 6. *Styphelia subulata.* **A** Flower, external view; **B** flower, internal view. Scale bar = 1 mm. — *M. Hislop 4189*. Drawings by Hung Ky Nguyen.

Distribution and habitat. Widely distributed in the Mallee, Esperance Plains and Coolgardie bioregions with a couple of records in the Avon Wheatbelt; from the Stirling Range in the west, eastwards to Israelite Bay and north to Quairading and the Koolyanobbing area (Fig. 7). *Styphelia subulata* favours low-lying country, most frequently in the vicinity of salt lakes and saline water courses, but one record has it growing on the edge of a breakaway. Occurs in various woodland or heathland communities, mostly in sandy soils. Associated species are frequently halophytic.

Phenology. The main flowering period is from April to June with mature fruit present at least between September and November.

Conservation status. Widespread and locally common. No conservation code is recommended here.

Affinities. *Leucopogon subulatus* was treated by Bentham (1868) as a taxonomic synonym of *L. insularis*, and the name has not been used since that time. Morphological similarities between the two species however, are superficial and in the phylogenetic tree of Puente-Lelièvre *et al.* (2016) they were placed in different groups: *Styphelia insularis* in Group V and *S. subulata* (as *L.* sp. Kau Rock) in Group III. The two can be readily distinguished by a number of differences including leaf morphology (abaxial surfaces deeply grooved and hairy in *S. subulata*, *cf.* smooth to very shallowly grooved and more or less glabrous in *S. insularis*) and corolla indumentum (internal corolla tube hairy in *S. subulata*, *cf.* glabrous in *S. insularis*).

The phylogenetic tree of Puente-Lelièvre *et al.* (2016) showed a well-supported sister relationship between *Styphelia subulata* (as *L.* sp. Kau Rock) and *S. intertexta*. The former is easily distinguished from *S. intertexta*, as well as *S. deserticola* and *S. saxicola*, by virtue of its much shorter style and filaments: the style being included in the corolla tube and the anthers usually partially included, or sometimes barely exserted (*cf.* style and anthers long-exserted from the tube in the other three members of the group).

Non-flowering specimens of *Styphelia subulata* can be difficult to distinguish from *S. intertexta*. Usually however, there is a useful, although often subtle, difference in the adaxial leaf surfaces. In the dried leaves of most collections of *S. subulata* one to three longitudinal grooves are clearly evident whereas in *S. intertexta* the grooves are mostly not present, or if so, are very indistinct. The fruit shape of *S. subulata* is also more variable, with ellipsoid and more or less globose fruit both common. In *S. intertexta* the fruit is apparently always ellipsoid.

There are similarities between *Styphelia subulata* and *S. intertexta* in some aspects of their morphological variability. The branchlet indumentum of *S. subulata* is of the same two types described above for *S. intertexta*, except that in the former it is the longer hair type that is the more restricted, apparently occurring only in the south-east of the species' range. Adaxial leaf rugosity also varies considerably in *S. subulata*, to an even greater extent than in *S. intertexta*. Populations in the south-west of the species' range have almost smooth adaxial surfaces, whereas in some northern populations the rugosity is so extreme that the surfaces are more or less transversely ridged. Another variable character that the two species share is the presence of hairs on the lower style. But while in *S. intertexta* hairy styles are relatively common, in *S. subulata* they are rare.

Although the geographic range of *Styphelia intertexta* is nested almost entirely within that of the more widely distributed *S. subulata*, there are no records of the two co-occurring at the same site. In large part this is likely to be because of a different habitat preference, with *S. intertexta* avoiding the low flats usually favoured by *S. subulata*.

Notes. It seems highly likely that the different presentation of anthers and stigma in *Styphelia subulata* is indicative of a different pollination strategy. For example exserted anthers and style have been associated with preferential visitation by butterflies and moths (Keighery 1996). It is also likely to be significant in this regard that, while the flowers of *S. intertexta* are odourless, those of *S. subulata* are sweetly scented (*pers. obs.*). The co-occurrence in this group of species with both floral configurations highlights the artificiality of the previous morphological distinction between *Styphelia* and *Leucopogon*, and indeed the caution needed in using these characters to define any rank higher than species level.

Selected specimens examined

WESTERN AUSTRALIA: Polar Bear Peninsula, Lake Cowan, Norseman, 20 Aug. 2002, *R. Butler RB 31* (PERTH); 8.5 km E of Point Malcolm Rd on Fisheries Rd, where track hits N margin of Daringdella Lake, Nuytsland Nature Reserve, 20 Apr. 1993, *G.F. Craig 2534* (NSW, PERTH); 5.8 km S of Rabbit Proof Fence, E of Hyden, 9 Apr. 1997, *R. Cranfield 11267B* (PERTH); Israelite Bay, 6.3 km NE of Fisherman's shack on main track, 18 May 2002, *M. Hislop & F. Hort MH 2628* (PERTH); Kumarl–Lake King Rd, 8.4 km from Esperance–Norseman Rd, then 150 m N to shoreline of Lake Exclamation, 21 May 2002, *M. Hislop & F. Hort MH 2659* (PERTH); railway maintenance track, 25.4 km E of Southern Cross–Koolyanobbing Rd, then 500 m SW to edge of salt lake, 18 May 2004, *M. Hislop & F. Hort MH 3184* (NSW, PERTH); Lagoon Rd, 3.1 km N of Kendall Rd, E of Scaddan, 22 May 2004, *M. Hislop & F. Hort MH 3218* (PERTH); Chinocup Nature Reserve, 4.8 km E of Chinocup Rd along main access track, 24 May 2004, *M. Hislop & F. Hort MH 3238* (CANB, PERTH); Stirling Range National Park, Salt River Rd, 3.7 km W of Formby South Rd, 23 Apr. 2005, *M. Hislop 3437* (CANB, K, PERTH); Stirling Range National Park, Salt River Rd, 3.7 km W of Formby South Rd, 31 Aug. 2005, *M. Hislop 3493* (CANB, PERTH); southern shores of Lake Baladjie, NE of Baladjie Rock, NW of Bullfinch, 15 Apr. 2006, *M. Hislop 3573* (CANB, NSW,

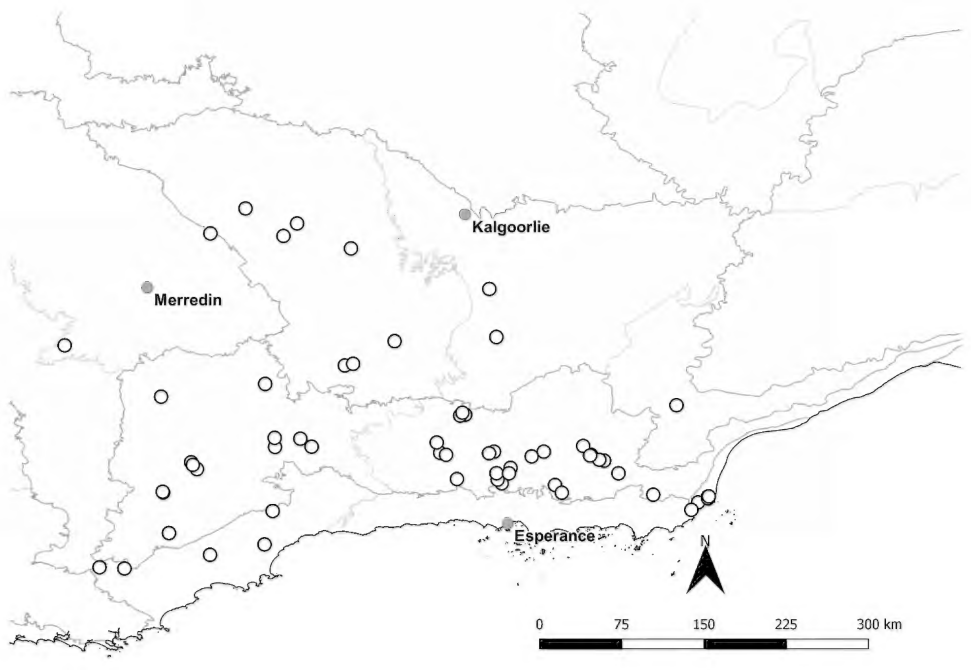

Fig. 7. Distribution of *Styphelia subulata* in Western Australia.

PERTH); W side of Styles Rd, 6.9 km S of Ridley Rd, SE of Grass Patch, 9 May 2012, *M. Hislop 4189* (CANB, K, MEL, PERTH); S of Quairading on private property, 29 Mar. 2016, *B. Hort NM 209* (PERTH); on W boundary of the reserve, 200 m S of Mallee Rd & Hill Rd junction, Lakelands Nature Reserve, c. 33 km SW of Newdegate, 17 May 1999, *G.J. Keighery & N. Gibson 4152* (PERTH); 1.5 km E of McDermid Rock, c. 97 km W of Norseman, 11 July 1979, *K.R. Newbey 5247* (PERTH); Cowerlalup [Cowalellup] Reserve, 20 km S of Ongerup on Boxwood Hill–Ongerup Rd, 8 May 2005, *S. Oborne 74* (PERTH); Clyde Rock area [NE of Condingup], 5 Sep. 1986, *J.M. Powell s.n.* (HO, K, NSW, PERTH); Kau Rock Nature Reserve, Mount Ney Rd, 1.4 km from Kau Rock Rd [N of Condingup], 8 Apr. 2012, *K.R. Thiele 4493* (NSW, PERTH).

Acknowledgements

I would like to thank Hung Ky Nguyen for the excellent line drawings, Steve Dillon for generating the distribution maps and Natalie Murdock, formerly of Mattiske Consulting, for systematically collecting *S. deserticola* during visits to the Great Victoria Desert, and without whose collections the description of that species would have been much less complete.

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A preliminary survey of the leaf-indumentum in the Australian Pomaderreae (Rhamnaceae) using Scanning Electron Microscopy

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Abstract: The tribe Pomaderreae (10 genera, c. 240 species) is almost endemic to Australia and defined within Rhamnaceae by the presence of 'stellate hairs'. This paper is the first to report observations on the leaf-indumentum of 33 species of the tribe with Scanning Electron Microscopy. Apart from simple hairs and papillae, three types of stellate trichomes were observed: fasciculate hairs, appressed stellate hairs and multiradiate hairs (sessile or stalked). The existence of stellate trichomes on the examined species of Pomaderreae was confirmed. Trichomes and indumenta are often variable within genera, as the type of indumentum may be more related to its function. Some groups of species in the genera *Cryptandra* Sm., *Pomaderris* Labill. and *Stenanthemum* Reissek have indumentum characters that seem to be more consistent and might be of value to elucidate relationships between taxa.

Keywords: Rhamnaceae, Pomaderreae, leaf morphology, trichomes, hairs, leaf surface, SEM

Introduction

Pomaderreae Reissek ex Endl. is the second largest tribe of Rhamnaceae. It was first described by Reissek (1840), but not accepted by subsequent botanists (e.g. Hooker 1862; Suessenguth 1953), until Richardson *et al.* (2000b) revised the suprageneric classification of the family. The tribe is now defined by the presence of 'stellate hairs' on stems, leaves and/or flowers; schizocarpic capsules with 1-seeded fruitlets are also a characteristic of, but not unique to, Pomaderreae.

The tribe is highly supported in all molecular analyses of the family (Richardson *et al.* 2000a; Onstein *et al.* 2015; Hauenschild *et al.* 2016, 2018; van Santen & Linder 2020), however the backbone of these phylogenies is not fully resolved and the exact relationship to other tribes is unknown. Pomaderreae seems to be most closely related to the tribe Colletieae (mainly distributed in South America, New Zealand and south-eastern Australia) and *Schistocarpaea johnsonii* F.Muell. (endemic to northern Queensland), as well as the *Alphitonia* Group (comprising the closely related genera *Alphitonia* Reissek ex Endl., *Granitites* Rye, *Jaffrea* H.C.Hopkins & Pillon and *Emmenosperma* F.Muell.; Hopkins *et al.* 2015).

Pomaderreae is virtually endemic to Australia, with only eight species of *Pomaderris* Labill. occurring in New Zealand. Most taxa are distributed in the temperate to semi-arid regions of south-western and south-eastern Australia, some occur in the tropical north of the continent and in the arid centre. Many species have xeromorphic adaptations, such as small, hard, revolute or conduplicate leaves, a dense indumentum or spines.

On-going molecular and morphological studies in the Australian Rhamnaceae have already resulted in the revision of the generic limits within Pomaderreae (Rye 1995a, 2001; Kellermann *et al.* 2005, 2006, 2007). There are currently approximately 240 species recognised in ten genera: *Blackallia* C.A.Gardner (1 species), *Cryptandra* Sm. (c. 55), *Papistylus* Kellermann, Rye & K.R.Thiele (2), *Polianthion* K.R.Thiele (4), *Pomaderris* (75–80), *Serichonus* K.R.Thiele (1), *Siegfriedia* C.A.Gardner (1), *Spyridium* Fenzl (c. 50), *Stenanthemum* Reissek (c. 30) and *Trymalium* Fenzl (13).

While all genera receive high support in molecular analyses of the tribe (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Kellermann & Udovicic 2008; Nge *et al.* 2019; see also Richardson *et al.* 2000a; Onstein *et al.* 2015; Hauenschild *et al.* 2016, 2018; Fig. 12), the relationship between the genera, i.e. within the tribe, are unresolved, with the exception of a sister relationship of *Siegfriedia* and *Pomaderris* and a close relationship of the three small genera, *Blackallia*, *Papistylus* and *Serichonus*. A relationship of *Trymalium* to *Pomaderris*/*Siegfriedia* is supported in some analyses (Onstein *et al.* 2015; Hauenschild *et al.* 2016).

When Labillardiére (1804) described the first two species of *Pomaderris*, he noted the presence of fasciculate trichomes. Stellate trichomes of *Pom. apetala* Labill. were first illustrated by Brongniart (1826), without realising that they were a common character of *Pomaderris* and related genera. Botanists, such as Fenzl

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(1837), Steudel (1845) and Reissek (1848, 1857) were aware of the presence of stellate trichomes on Australian Rhamnaceae. Reissek (1840) even mentioned stellate indumentum as a generic character for *Pomaderris* and *Trymalium*, but not for *Cryptandra* and *Spyridium*. In his definition of Pomaderreae he also only included the former two genera.

It was Baillon (1875, 1880) who recognised that these genera "belonged to a distinct subseries, exclusively oceanic, [...] generally tomentose, with a simple or stellate, whitish or rusty down [i.e. indumentum]" (Baillon 1880: 61). Weberbauer (1895: 395) reported unpublished anatomical results by Emil Krause and stated that "der Besitz von Sternhaaren die australischen Gattungen *Pomaderris*, *Trymalium*, *Spyridium*, *Cryptandra* vor allen anderen [...] auszeichnet" ["the presence of stellate hairs characterises the Australian genera *Pomaderris*, *Trymalium*, *Spyridium*, *Cryptandra* from all others"]. Four years later, Wildeman (1899: 31) describes *Pom. racemosa* as having "un tomentum forme de poils étoilés" ["an indumentum consisting of stellate hairs"] and illustrates one trichome in close-up. Grès (1901) confirmed these observations on *Pom. apetala* and *Pom. aspera* and published a detailed illustration of a cross section through a leaf including stellate trichomes (Fig. 1).

Gemoll (1902) and Herzog (1903) conducted detailed leaf anatomical examinations on all tribes of Rhamnaceae. Gemoll (1902) observed stellate trichomes on all 32 examined species of Pomaderreae and classified them into four types, grouped in two pairs (Table 1). Gemoll's results for the tribe are summarised in Table 2 (as they were so far largely inaccessible to researchers in Australia). Subsequent authors, for example Suessenguth (1953), generally agreed that the 'Australian stellate-haired Rhamnaceae' belonged to a distinct group within the family.

Since Gemoll (1902) and Herzog (1903) no studies have been published on leaf anatomy and the indumentum of the leaves of Pomaderreae. Observations are usually scattered through taxonomic papers and descriptions of new species (e.g. Walsh 1990; Rye 1995a, b; Walsh & Coates 1997; Thiele & West 2004; Thiele 2007; Kellermann & Barker 2012). Moore (1986) gave schematic drawings of the indumentum on leaves of New Zealand species of *Pomaderris*. Notable are the studies by Peacock (1987), who examined and photographed trichomes in the *Pom. aspera-apetala* complex, and Ross (1990) with her study on five species of *Pomaderris* in Queensland, in which she documents the indumentum of each species. The latter publication is the only one that gives detailed descriptions and illustrations (line drawings) of the indumentum.

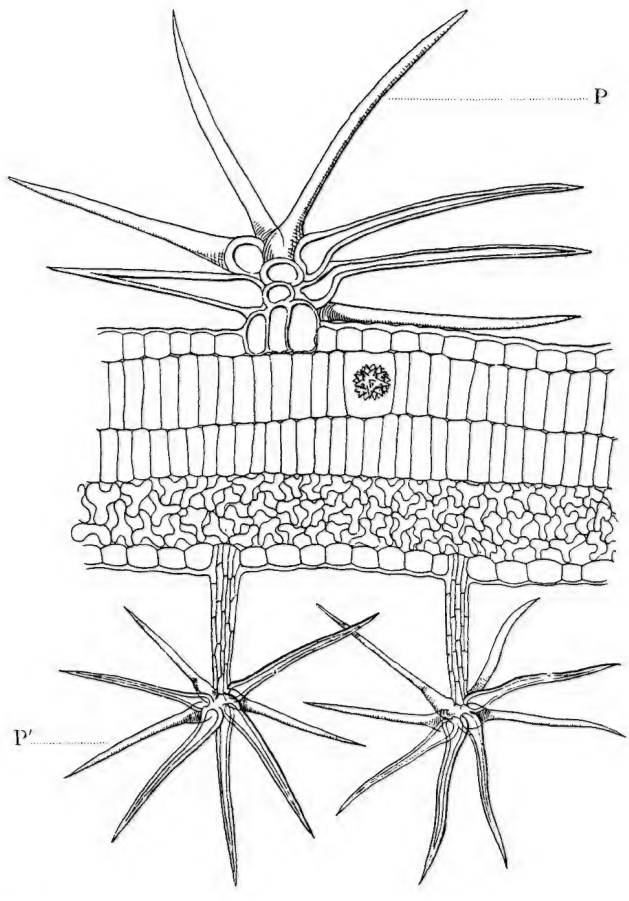

Fig. 1. Cross-section through leaf of *Pomaderris apetala*, showing multiradiate hairs on the upper surface (**P**) and dendroid hairs on the lower surface (**P'**). Reproduced from Grès (1901).

Table 1. The types of stellate trichomes reported by Gemoll (1902).

I – Stellate trichomes with a short stem/stalk:
IA – Stem narrow, inserted in epidermis
IB – Stem broad, multicellular, sitting on epidermis (only *Pomaderris apetala*)
II – Stellate trichomes with a long stem/stalk:
IIA – Stem consisting of long, stretched hair-cells, sitting on the epidermis (only *Spyridium coactilifolium*)
IIB – Stem made from numerous, specialised small cells, integrated in the epidermis (some *Pomaderris* spp.)

Different classification systems for plant hairs have been introduced, but terminology on trichomes and indumentum types is not standardised. Hewson (1988) uses two main categories: emergence and trichome. Emergences are defined as outgrowths that arise from more than one superficial cell and include papillae, tubercles, prickles or warts. Trichomes are outgrowths without vascular tissue that originate from one epidermal cell. They consist of hairs, bristles, prickles, scales and other hair-like outgrowths, and can be single- or multi-cellular.

Table 2. Trichomes reported by Gemoll (1902) for 32 species of Pomaderreae. Abbreviations: IA, IB, IIA, IIB, Gemoll's types of stellate trichomes (Table 1); +, trichome type is present; ?, questionable presence; Sgl., simple trichomes (L and S denote long and short simple trichomes); Pap., papillae. If Gemoll indicated the number of arms of trichome type IA, then this is indicated (e.g. '2, 4'). Gemoll's voucher specimens for most of the taxa can be found at the Herbarium in Munich, Germany (M).

Species name in Gemoll[1]	Currently recognised name	Lower surface of leaf						Nerves on lower surface						Upper surface of leaf					
		IA	IB	IIA	IIB	Sgl	Pap	IA	IB	IIA	IIB	Sgl	Pap	IA	IB	IIA	IIB	Sgl	Pap
Cryptandra obovata Sieber	*Pultenaea altissima* F.Muell. ex Benth.																		
C. sieberi Fenzl	*C. amara* Sm.											L						+	
C. arbutifolia Fenzl	*C. arbutifolia* Fenzl var. *arbutiflora*											L						+	
C. australis Sm.	*C. ericoides* Sm.	+						?										+	
C. leucopogon Meisn.	*C. leucopogon* Meisn. ex Reissek	+						?										+	
C. glabrata Stdl.	*C. arbutiflora* var. *tubulosa* (Fenzl) Benth.																	+	
C. mutila Nees	*C. mutila* Nees ex Reissek	+				S					S								
C. scoparia Reiss.	*C. scoparia* Reissek	+						?										+	
C. spinescens Sieber	*C. spinescens* Sieber ex DC.	+										L							
C. tomentosa Lindley	*C. tomentosa* Lindley	+						+				L	2, 3					+	
Pomaderris apetala Lab.	*Pom. apetala* Labill.		+		+	L			?		?	?				+			
Pom. discolor Vent.	*Pom. discolor* (Vent.) Poir	+										+	2, 3				+		
Pom. elliptica Labill.	*Pom. elliptica* Labill.	+										L					+		
Pom. phylliraeoides Sieb.	*Pom. phillyreoides* Sieb. ex DC.	+				+		+				+					S		
Pom. ferruginea Sieb.	*Pom. ferruginea* Sieb ex Fenzl	+										+					+		
Pom. lanigera Sims	*Pom. lanigera* (Andrews) Sieber ex Sims	+										L					+		
Pom. ligustrina Sieber	*Pom. ligustrina* Sieber ex DC.	+										L					+		
Pom. phylicaefolia Link.	*Pom. phylicifolia* Lodd. ex Link	+										L					S		
Pom. prunifolia Cunn.	*Pom. prunifolia* A.Cunn ex Fenzl	+									+						S		
Pom. racemosa Hook.	*Pom. racemosa* Hook. or *P. oraria* F.Muell.	+									+								
C. coactilifolia F.v.Müller	*Spyridium coactilifolium* Reissek			+											+				
C. eriocephala Hook.	*Sp. eriocephalum* Fenzl	+						+				L					S		
Trymalium globulosum Fenzl	*Sp. globulosum* (Labill.) Benth.	+						?									+		
C. gunii Hook.	*Sp. gunnii* (Hook.f.) Benth.	+						?											
C. obcordata Hook.	*Sp. obcordatum* (Hook.f.) W.M.Curtis	+						+				L							
Sp. parvifolium F.Müller	*Sp. parvifolium* (Hook.) F.Muell	+						?									+		
T. parvifolium F.Muell.	*Sp. parvifolium* (Hook.) F.Muell.	+											2, 4				+		
T. majoranaefolium Fenzl	*Sp. spadiceum* var *majoranifolium* (Fenzl) Benth.	+						?					2, 4				+		
C. ulicina Hook.	*Sp. ulicinum* (Hook.) Benth.	+																	
C. vexillifera Hook.	*Sp. vexilliferum* (Hook.) Reissek	+						?				+							
C. floribunda Steudl.	*T. ledifolium* Fenzl var. ledifolium	+						+				L	4						
T. floribundum Steudel	*T. odoratissimum* Lindl. subsp *odoratissimum*	+						?									+		
T. fragans Fenzl	Possibly *T. odoratissimum* Lindl.	+											2					+	

[1] The name "*Trymalium fragans* Fenzl" is of horticultural origin and could only be found in a list of cultivated species (Koch 1858), in some publications, the name is spelt "*Trymalium fragrans*" and attributed to "h. Kew" (Otto 1845, 1849); it is possibly identical with *Trymalium odoratissimum* Lindl. *Cryptandra obovata* Sieber ex DC. is actually a species of Fabaceae, *Pultenaea altissima* F.Muell. ex Benth. (Kok & West 2002).

Table 3. Sources of plant material used for SEM. ANBG: Australian National Botanic Gardens, Canberra.

Species	Locality	Voucher specimen
Blackallia nudiflora (F.Muell.) Rye & Kellermann	W.A.: Northampton	*J. Kellermann 260* (MEL)
Cryptandra amara Sm.	N.S.W.: Ebon Falls	*D.B. Foreman 2129* (MEL)
C. connata (C.A.Gardner) C.A.Gardner	W.A.: Brealya Well	*S. Patrick 2273* (PERTH)
C. dielsii C.A.Gardner ex Rye	W.A.: Trayning-Kellerberrin Rd	*J. Kellermann 292* (MEL)
C. intermedia (Rye) Rye	W.A.: Pobaderry Road	*J. Kellermann 311* (MEL)
C. intratropica W.Fitzg.	W.A.: King Edward River	*L.A. Craven & C.L. Brubaker 9163* (PERTH)
C. lanosiflora F.Muell.	ANBG 617457 Sect. 99F	*S. Fethers 8, I.R. Telford & S. Pedersen* (CANB)
C. mutila Nees ex Reissek	W.A.: S of Freemantle	*A.S. George 9185* (MEL)
Papistylus grandiflorus (C.A.Gardner) Kellermann, Rye & K.R.Thiele	W.A.: Peterwangi Hill	*J. Kellermann 274* (MEL)
Polianthion bilocularis (A.S.George) Kellermann	W.A.: Dongolocking	*S. Patrick 394* (PERTH)
Pol. collinum Rye	W.A.: Yalgoo	*A. Chant 9* (PERTH)
Pol. minutiflorum (E.M.Ross) K.R.Thiele	Qld: Coominglah State Forest	*A.R. Bean 9107 & G. Turpin* (CANB)
Pol. wichurae (Nees ex Reissek) K.R.Thiele	W.A.: Hi Vallee Farm, Badgingarra	*J. Kellermann 183* (MEL)
Pomaderris angustifolia N.A.Wakef.	Vic.: Barkly River	*E.A. Chesterfield 3524* (MEL)
Pom. apetala Labill.	Vic.: Mafeking	*R.J. Peacock 215* (MEL)
Pom. aspera Sieb. ex DC.	Vic.: Kalimna	*J. Stephen 6* (MEL)
Pom. brevifolia N.G.Walsh	W.A.: Ravensthorpe	*J. Kellermann 388* (MEL)
Pom. elliptica Labill.	Vic.: Wonga Park	*D.J. van Bockel 344* (MEL)
Pom. obcordata Fenzl	S.A.: Eyre Peninsula	*N.G. Walsh 3999* (MEL)
Pom. racemosa Hook.	Vic.: Kentbruck	*I. Hore-Lang s.n.* (MELU)
Serichonus gracilipes (Diels) K.R.Thiele	W.A.: Northampton	*J. Kellermann 262* (MEL)
Siegfriedia darwinioides C.A.Gardner	W.A.: Ravensthorpe	*J. Kellermann 391* (MEL)
Spyridium burragorang K.R.Thiele	ANBG c606176 Sect. 31	*S. Donaldson 903* (CBG)
Sp. daltonii (F. Muell.) Kellermann	Vic.: Grampians	*P. G. Neish 397* (MEL)
Sp. furculentum W.R.Barker & Kellermann	Vic.: near Little Desert	*A.C. Cochrane 71, N.G. Walsh & J.G. Eichler* (MEL)
Sp. globulosum (Labill.) Benth.	W.A.: Neerabup Natl Park	*J. Kellermann 172* (MEL)
Sp. parvifolium (Hook.) F. Muell.	Vic.: Grampians	*J. Kellermann 124* (MEL)
Stenanthemum centrale K.R.Thiele	N.T.: Palm Valley	*D.V. Matthews s.n.* (MEL)
St. leucophractum (Schldl.) Reissek	Vic.: Pink Lakes State Park.	*E.A. Chesterfield 1828* (MEL)
Trymalium ledifolium var. *rosmarinifolium* (Steud.) Benth	W.A.: Flynn State Forest, York	*J. Kellermann 294* (MEL)
T. monospermum Rye	W.A.: Narrogin	*L.W. Sage 1540* (MEL)
T. odoratissimum subsp. *trifidum* (Rye) Kellermannn, Rye & K.R.Thiele	W.A.: Two Peoples Bay Natl Park	*J. Kellermann 398* (MEL)
T. wayi F.Muell. & Tate	S.A.: E of Crystal Brook	*D.N. Kraehenbuehl 5194* (CANB)

Trichomes can form a sparse to dense indumentum on all above-ground parts of a plant. The indumentum on the upper and lower surface of the leaves is of particular importance due to the variety of functions that it performs. It has been traditionally used in taxonomic studies in Brassicaceae (e.g. Rollins & Banerjee 1976; Ančev & Goranova 2006), Fabaceae (e.g. Lackey 1978; Zarre 2003), Fagaceae (e.g. Jones 1986; Ávalos & Salinas 2003; Tschan & Denk 2012), Myrtaceae (e.g. Ladiges 1984), Solanaceae (e.g. Roe 1971, Granada-Chacón & Benítez de Rojas 2005) and other groups. Surveys of trichomes for the whole plant kingdom were published by Uphof (1962), Hummel & Staesche (1962) and Napp-Zinn (1973), however, information on Rhamnaceae and Pomaderreae is very limited in these books.

This paper examines, for the first time, the trichome diversity in Pomaderreae with Scanning Electron Microscopy (SEM). It gives an overview of the variation

of indumenta and types of trichomes observed in the tribe, using a selected sample of 33 species from all currently accepted genera, and draws some conclusions on the systematic usefulness of indumentum characters.

Materials and methods

Thirty-three species of Pomaderreae were examined using Scanning Electron Microscopy. Only material from herbarium specimens was used (Table 3).

The material was placed in silica gel overnight to remove residual moisture. Samples of leaves (both surfaces, and a cross-section), stems and stipules were mounted on aluminium stubs using double-sided carbon tabs and coated with gold using an Edward's S150B Sputter Coater. Samples were viewed under a Phillips XL30 Field Emission Scanning Electron Microscope.

Micrographs were taken of the upper and lower surface of the leaves and from cross sections. If no indumentum was present on the upper surface, pictures of epidermal features were taken at higher resolution. Three to five pictures were taken for each surface and typical examples for each species were chosen for Figures 3–11. Descriptions of the general indumentum and of the type of trichomes were written for each species. The results were also tabulated (Tables 4–6) and combined with Ross' observations on five Queensland species of *Pomaderris* (Ross 1990).

Data for the species examined is presented and discussed in alphabetical order, but in the figures, related taxa are grouped together.

Results

Classification of trichomes

The following types of trichomes were identified in this study. Nomenclature of trichomes was mainly adapted from Jones (1986); for general descriptions of indumentum, the terminology of Hewson (1988) is used. Glandular trichomes were not observed on Pomaderreae. The distinction between the three types of stellate trichomes *sensu lato* (fasciculate, appressed stellate and multiradiate trichomes) is somewhat arbitrary and intermediate forms may be observed. Figure 2 shows simplified drawings of the trichome types.

Simple hairs (Fig. 2A–D). Trichomes of this type can vary considerably in length. They are unicellular. The trichomes are usually straight (e.g. Figs 4F, 10E), but can also appear wavy or curly (Fig. 2B). Most of the simple trichomes examined are sessile when they emerge from the epidermis. Some species bear simple hairs that have a ***pedestal***, i.e. the trichome grows from a distinctive rounded base (Fig. 2C).

Papillae (Fig. 2E). Although not strictly trichomes, the presence and distribution of papillae on the upper surface of some species was noted (e.g. Figs 5B, 11J).

Fasciculate hairs (Fig. 2F–I). These trichomes consist of two or more elements that are only joined at the base, i.e. they include ***bifid hairs*** (Fig. 2I). As such, they are multicellular trichomes. The rays may be erect (e.g. Fig. 3C) or spread out to a varying degree. Fasciculate hairs can be sessile or borne on a pedestal (Fig. 2G).

Appressed stellate hairs (Fig. 2J–L). Stellate trichomes in a strict sense are characterised by the possession of three or more rays (arms) that radiate "from a common point of attachment in a fashion parallel, or nearly parallel, to the leaf surface" (Jones 1986: 263).

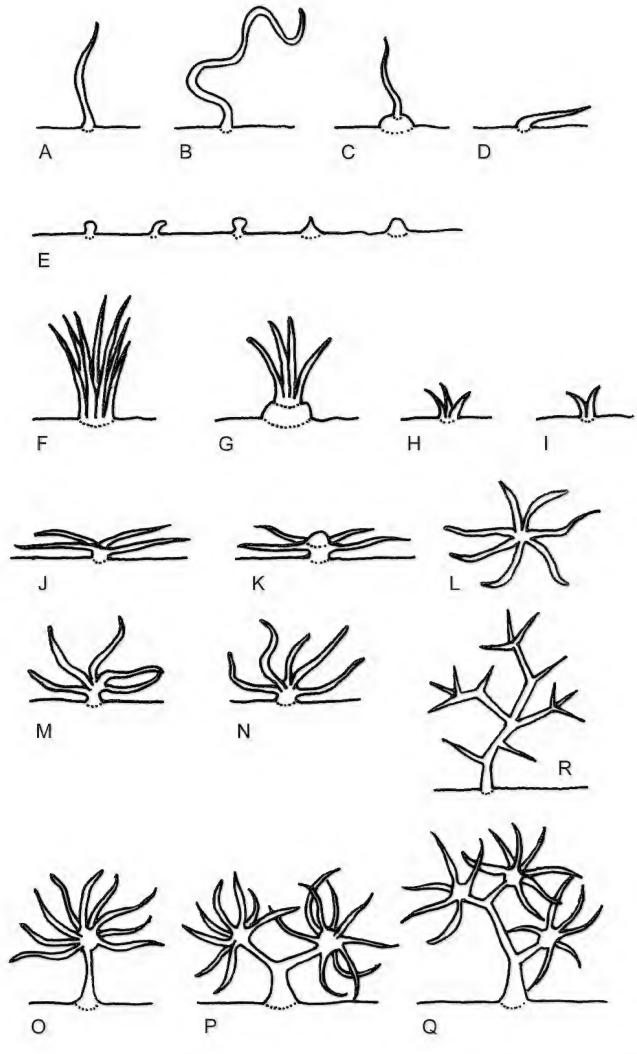

Fig. 2. Trichome classification. **A–Q** Trichome types in Pomaderreae. **A–D** Simple hairs: **A** straight trichome; **B** wavy or curly trichome; **C** trichome with pedestal; **D** appressed trichome. **E** papillae (several examples). **F–I** Fasciculate hairs: **F** trichome with many rays; **G** trichome with pedestal; **H** tri-fid hair; **I** bi-fid hair. **J–L** Appressed stellate hairs: **J** without umbo; **K** trichome with umbo (umbonate); **L** view from above. **M–Q** Multiradiate hairs: **M**, **N** sessile trichomes; **O** stalked multiradiate trichome; **P** dendroid multiradiate trichome with two heads; **Q** dendroid trichome with three heads. **R** True dendritic hair (not in Pomaderreae).

They appear to be multicellular. The trichomes can be sessile and appressed to the leaf surface (e.g. Figs 8F, 11L), or be elevated from the surface on a pedestal. In some species, an umbo (Fig. 2K), as defined by Rollins & Banerjee (1976), was present; this is a mound at the centre of the stellate trichome (Fig. 8F). To avoid confusion with the term 'stellate', which is usually used in a broad sense, these stellate trichomes *sensu stricto* are here termed 'appressed stellate hairs'.

Multiradiate trichomes (Fig. 2M–O). This type of trichome consists of several to many rays (arms) that originate from a (usually) rounded common base in a "variety of seemingly random directions" (Jones 1986: 264). Multiradiate trichomes can be sessile (e.g. Fig. 9A), possess a pedestal, or sit on a multicellular stalk (Fig. 9C, F).

Dendroid trichomes (Fig. 2P, Q). In some species this stalk can be branched and carry two to four multiradiate 'heads'. These trichomes are called here 'dendroid trichomes' (Fig. 9K, L), to distinguish them from true 'dendritic hairs' (e.g. Roe 1971; Fig. 2R).

Surface sculpturing

In species with glabrous or near glabrous upper surfaces, it was possible to record the sculpturing on the epidermis. The following terms are used to describe the surface:

Wrinkled. The epidermis is irregularly and randomly folded, without any discernible pattern (e.g. Fig. 6D).

Striate. There are more or less parallel or irregularly arranged ridges visible on the surface (e.g. Figs 4G, 11A).

Punctate. Each epidermal cell is covered with small warty emergences, which gives the whole cell surface a spotted appearance (e.g. Fig. 10D).

Description of foliar trichomes and surfaces for each species

An asterisk behind the name of a species indicates that only limited information was available from SEM. Data from Ross (1990) for six species of *Pomaderris* is incorporated into these descriptions. Some of this information is summarised in Tables 4–6.

Note that the descriptions provided here apply strictly to the specimens examined with SEM (Table 3). Some species may have varying levels of pubescens, especially on the upper leaf surface.

Blackallia nudiflora (Fig. 6G–I)

Upper surface: Glabrous, with deep wrinkles throughout.

Lower surface: Densely silky (to villose) indumentum of c. 300 µm long simple antrorse hairs overlying smaller appressed stellate hairs with 3–6 rays (rays 100–150 µm long), some trichomes are bifid. Leaves glabrescent with age, retaining only simple hairs on the lower surface.

Cryptandra amara (Fig. 10D–E)

Upper surface: Glabrous, epidermis punctate.

Lower surface: Glabrous. Midrib with sparse antrorse strigose simple hairs, c. 500 µm long.

Although stellate trichomes are absent on the leaves of *C. amara*, stellate trichomes are numerous on flowers and young stems of this species, indicating its correct placement in Pomaderreae.

Cryptandra connata (Fig. 11J–L)

Upper surface: Glabrous, folded (but this might be due to shrinkage in herbarium material), epidermis punctate.

Lower surface: Densely tomentose with 2–4-armed fasciculate hairs (rays 50–100 µm long) and 5–8-armed multiradiate trichomes (rays 50–100 µm long). Midrib with 2–4-armed appressed stellate hairs (rays 40–80 µm long) and 250–400 µm long antrorse simple hairs.

Cryptandra dielsii (Fig. 11D–F)

Upper surface: Sparsely to moderately tomentose to hispid with 30–50 µm long simple hairs. Epidermis punctate.

Lower surface: moderately to densely tomentose indumentum of entangled 5–6-armed multiradiate hairs (rays c. 150 µm long).

Cryptandra intermedia (Fig. 10G–I)

Upper surface: Densely to moderately papillose, especially in young leaves. There is a gradient from papillae to simple hairs and 4–6-armed fasciculate trichomes (each with arms 50–100 µm long). Epidermis punctate.

Lower surface: Moderately to densely tomentose with 6–8-armed multiradiate and appressed stellate hairs (rays c. 100 µm long, each).

Cryptandra intratropica (Fig. 10J–L)

Upper surface: Densely tomentose indumentum of (3–) 4–10-armed multiradiate trichomes (rays 50–100 µm long).

Lower surface: Densely tomentose indumentum of 7–10-armed multiradiate trichomes (rays 50–100 µm long) with rays seemingly more slender than on upper surface. Midrib additionally with scattered 200–300 µm long antrorse simple hairs.

Cryptandra lanosiflora (Fig. 11A–C)

Upper surface: Glabrous. Epidermis parallel striate.

Lower surface: Densely tomentose indumentum of 5–10-armed fasciculate trichomes (40–80 µm long). Midrib with 5–10-armed appressed stellate hairs (rays 40–60 µm long) and c. 500 µm long antrorse simple hairs.

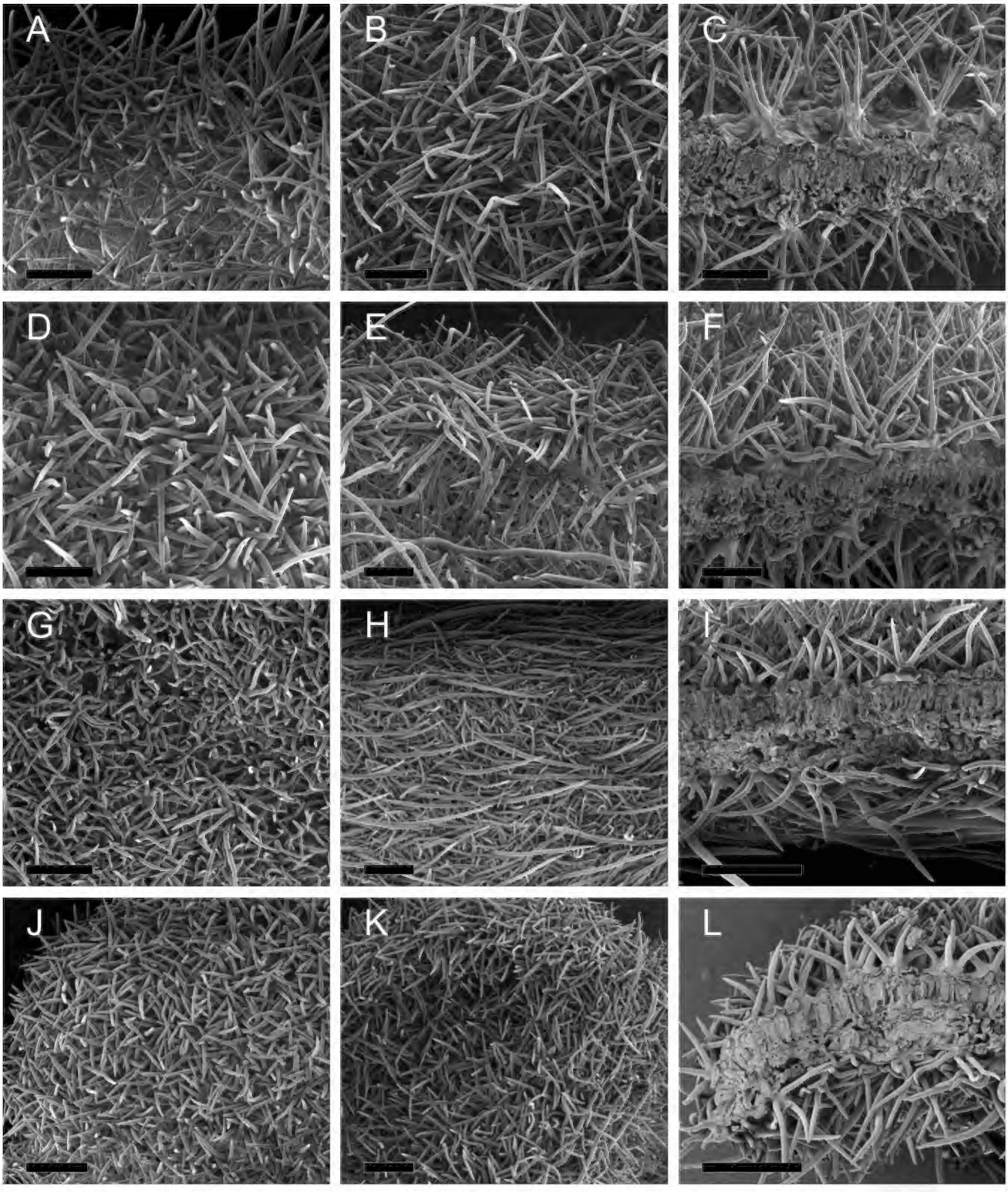

Fig. 3. Indumentum of leaves of *Polianthion*. **A–C** *Pol. wichurae*; **D–F** *Pol. bilocularis*; **G–I** *Pol. collinum*; **J–L** *Pol. minutiflorum*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm. Images first published in Kellermann *et al.* (2006).

Cryptandra mutila (Fig. 11J–L)

Upper surface: Sparsely papillose, surface slightly folded (but this might be due to shrinkage in herbarium material), epidermis punctate.

Lower surface: Glabrous. Midrib with sparse antrorse strigose simple hairs, c. 500 µm long, rarely with 4-armed appressed umbonate stellate hairs (rays c. 100 µm long).

Papistylus grandiflorus (Fig. 6D–F)

Upper surface: Glabrous with deep wrinkles throughout, occasionally trichomes on midrib.

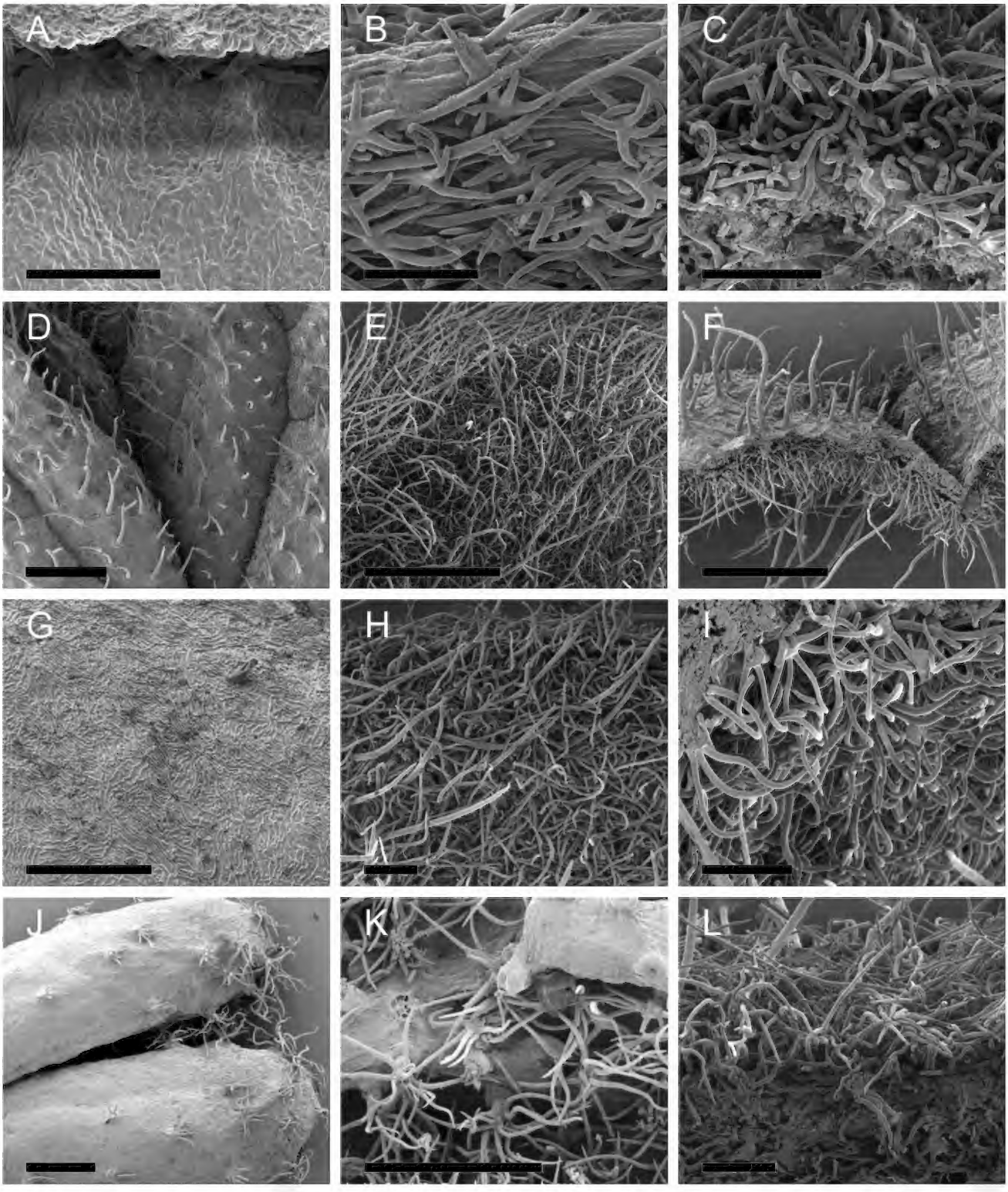

Fig. 4. Indumentum of leaves of *Spyridium*. **A–B** *Sp. globulosum*; **C–F** *Sp. parvifolium*; **G–I, L** *Sp. burragorang*; **J–K** *Sp. furculentum*. Vegetative leaves (**A–B**, **D–K**) and floral leaves (**C**, **L**). Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale A–C, G–I, K–L = 100 µm; D–F, J = 500 µm.

Lower surface: Densely silky (to villose) indumentum of c. 300 µm long appressed simple hairs overlying smaller umbonate appressed stellate hairs with possibly 4–6 rays (rays c. 200 µm long). The leaves glabrescent with age, retaining only a few trichomes on the lower surface and appressed antrorse trichomes along the midrib.

Polianthion bilocularis (Fig. 3D–F)

Upper surface: Densely tomentose indumentum of appressed stellate trichomes with 5–8 (–10) rays (rays 80–100 µm long) and slightly longer multiradiate hairs with 8–10 rays (rays 150–250 µm long).

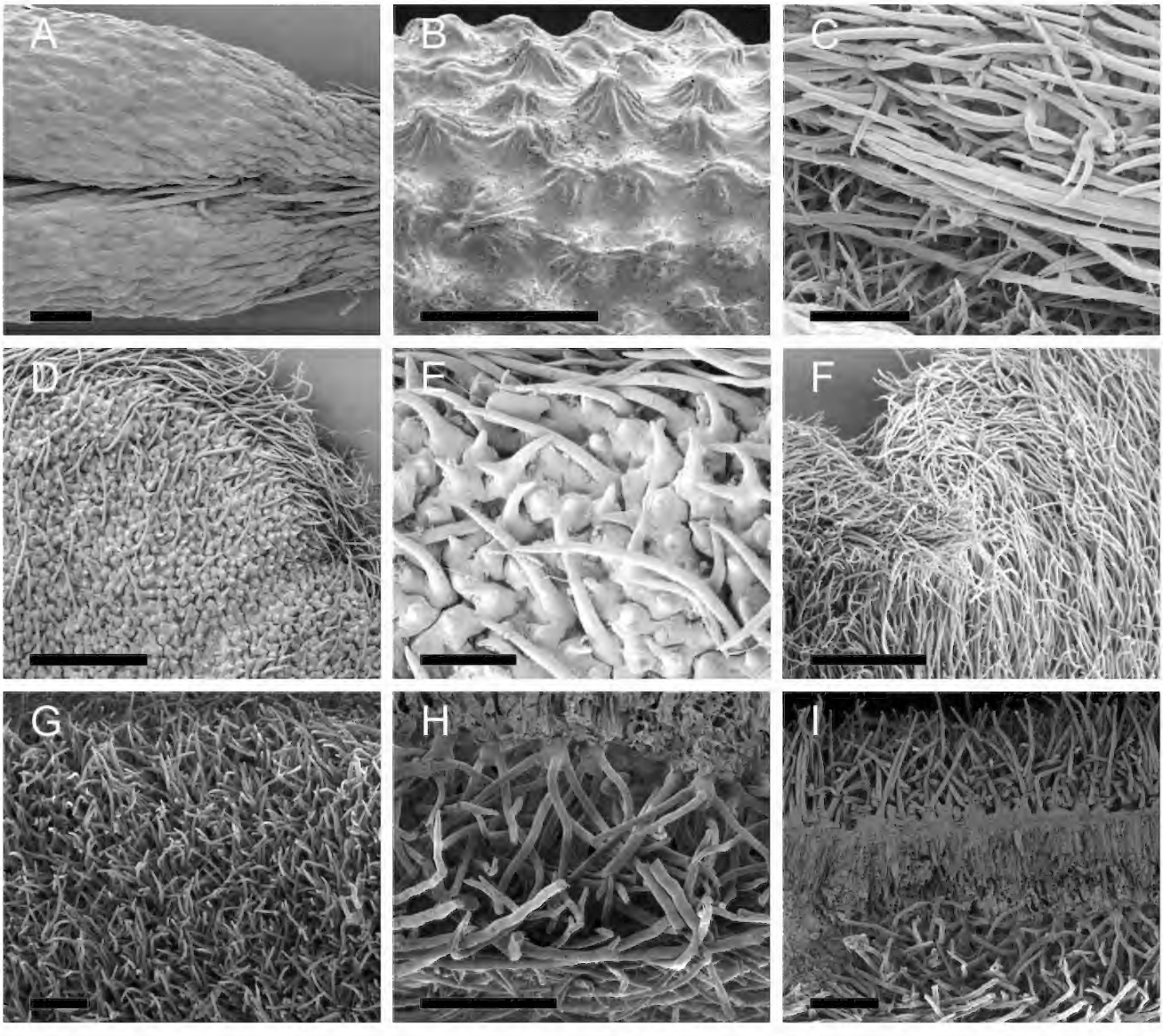

Fig. 5. Indumentum of leaves of *Spyridium* and *Stenanthemum*. **A–C** *Sp. daltonii*; **D–F** *St. leucophractum*; **G–I** *St. centrale*. Left column (**A**, **D**, **G**) & **B**, **E**, upper leaf surface; **C**, **F**, **H**, lower surface; **I**, cross section through leaf with upper leaf surface on top of the image. Scale A–C, E, G–I = 100 µm; D, F = 500 µm.

Lower surface: Densely tomentose to felty indumentum of appressed stellate trichomes with 6–8 (–10) rays (rays c. 100 µm long), slightly longer multiradiate hairs with 8–10 rays, each ray c. 200 mm long, and very long slightly wavy simple trichomes (c. 600 µm long).

Polianthion collinum (Fig. 3G–I)

Upper surface: Densely tomentose short indumentum of fasciculate trichomes with 2–4 (–8) rays (rays c. 50 µm long) and simple hairs of c. 50 µm length, both of which possess a slight pedestal.

Lower surface: Densely tomentose short indumentum of appressed stellate or slightly fasciculate trichomes with 4 rays, each ray 50–100 µm long overlain by c. 300 µm long antrorse simple hairs, which give the surface a velvety appearance.

Polianthion minutiflorum (Fig. 3J–L)

Upper surface: Densely tomentose indumentum of fasciculate trichomes with 2–6 rays (rays 50 µm long) and shorter 30–50 µm long simple hairs.

Lower surface: Densely tomentose indumentum of appressed stellate hairs with 4–8 rays of c. 100 µm in length, 4–8-armed multiradiate hairs (rays 100–200 µm long), and simple hairs that are appressed and 200–300 µm long along the midrib and c. 100 µm long elsewhere.

Polianthion wichurae (Fig. 3A–C)

Upper surface: Densely tomentose to felted indumentum of fasciculate trichomes with (5–) 8 (–10) rays (rays c. 100 µm long), which are slightly raised on a pedestal, and interspersed smaller simple hairs (c. 100 µm long).

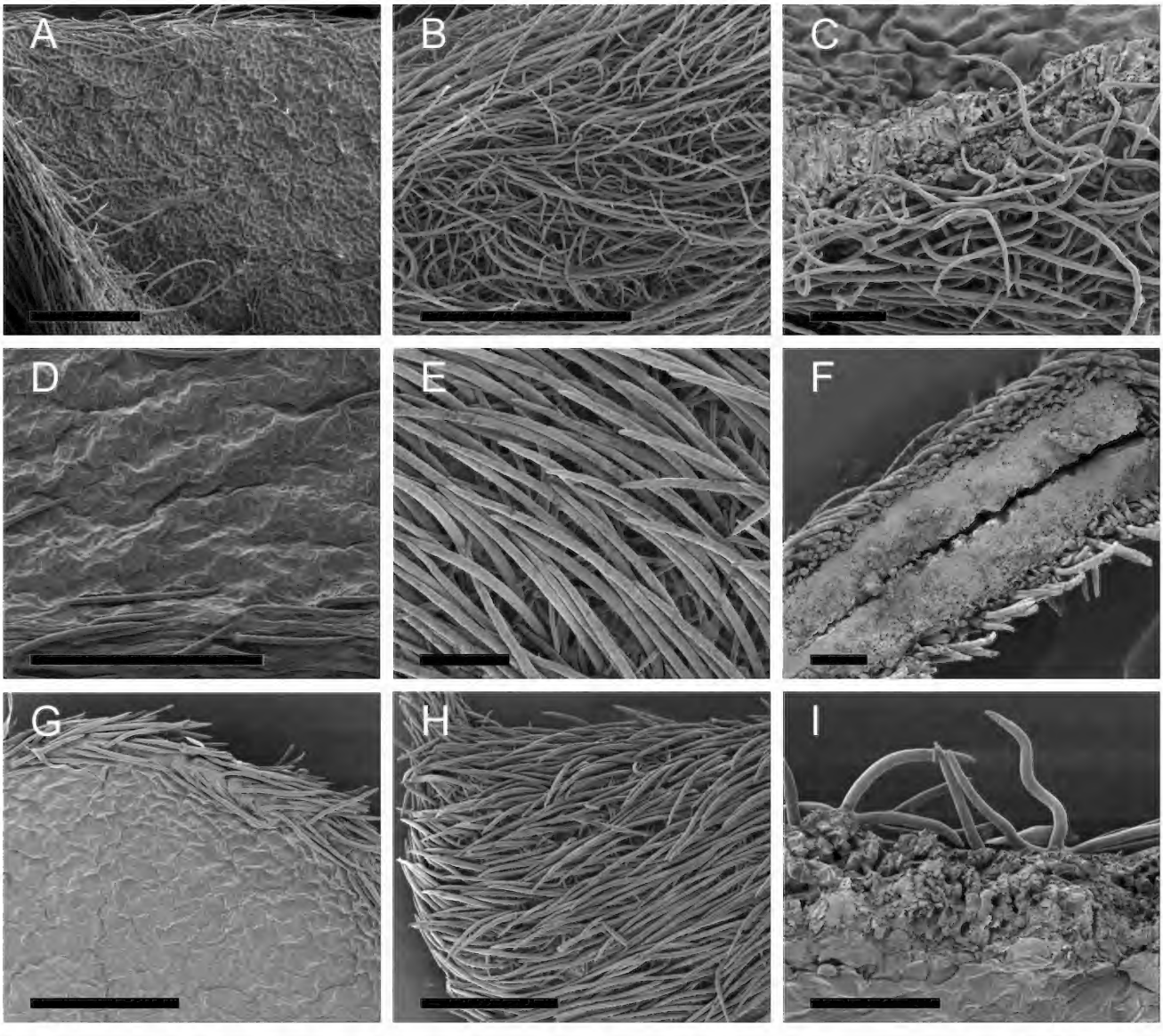

Fig. 6. Indumentum of leaves of species of three small Western Australian genera. **A–C** *Serichonus gracilipes*; **D–F** *Papistylus grandiflorus*; **G–I** *Blackallia nudiflora*. Left column (**A**, **D**, **G**), upper leaf surface; middle column (**B**, **E**, **H**), lower surface; right column, cross section through leaf with upper leaf surface on top of the image (**C**, **I**) or through conduplicate leaf (**F**). Scale C–F, I = 100 µm; A–B, G–H = 500 µm.

Lower surface: Densely to medium tomentose indumentum of multiradiate hairs with 8–10 arms, each arm c. 150 mm long.

Pomaderris angustifolia * (Fig. 8D–E)

Upper surface: Sparsely scattered 2–4-armed fasciculate hairs (rays c. 100 µm long) and 4–8-armed appressed stellate hairs with pedestal (rays c. 150 µm long). Surface pattern possibly striate.

Lower surface: Densely felted indumentum of 6–8-armed appressed umbonate stellate hairs (rays c. 100 µm long) and 4–8-armed multiradiate hairs with c. 200 µm long rays. Possibly some scattered simple hairs.

Pomaderris aspera (Fig. 9D–F, K–L)

Upper surface: Sparsely scattered 6–10-armed multiradiate hairs (rays 100–150 µm long). Surface irregular striate.

Lower surface: Densely felted indumentum of stalked and dendroid multiradiate trichomes with 6–40 rays per head (rays 200–250 µm long), and scattered c. 200 µm long simple hairs with pedestal. The surface can appear floccose when multiradiate heads break off.

Pomaderris apetala (Fig. 9A–C)

Upper surface: Scattered 10–20-armed multiradiate hairs (rays c. 200 µm in diameter). Surface smooth to irregular striate.

Lower surface: Densely felted indumentum of stalked and possibly dendroid multiradiate trichomes with 10–20 (–25) rays per head (rays 70–150 µm long) overlying 6–8-armed appressed umbonate stellate hairs (rays c. 70 µm long). The surface can appear floccose when multiradiate heads break off.

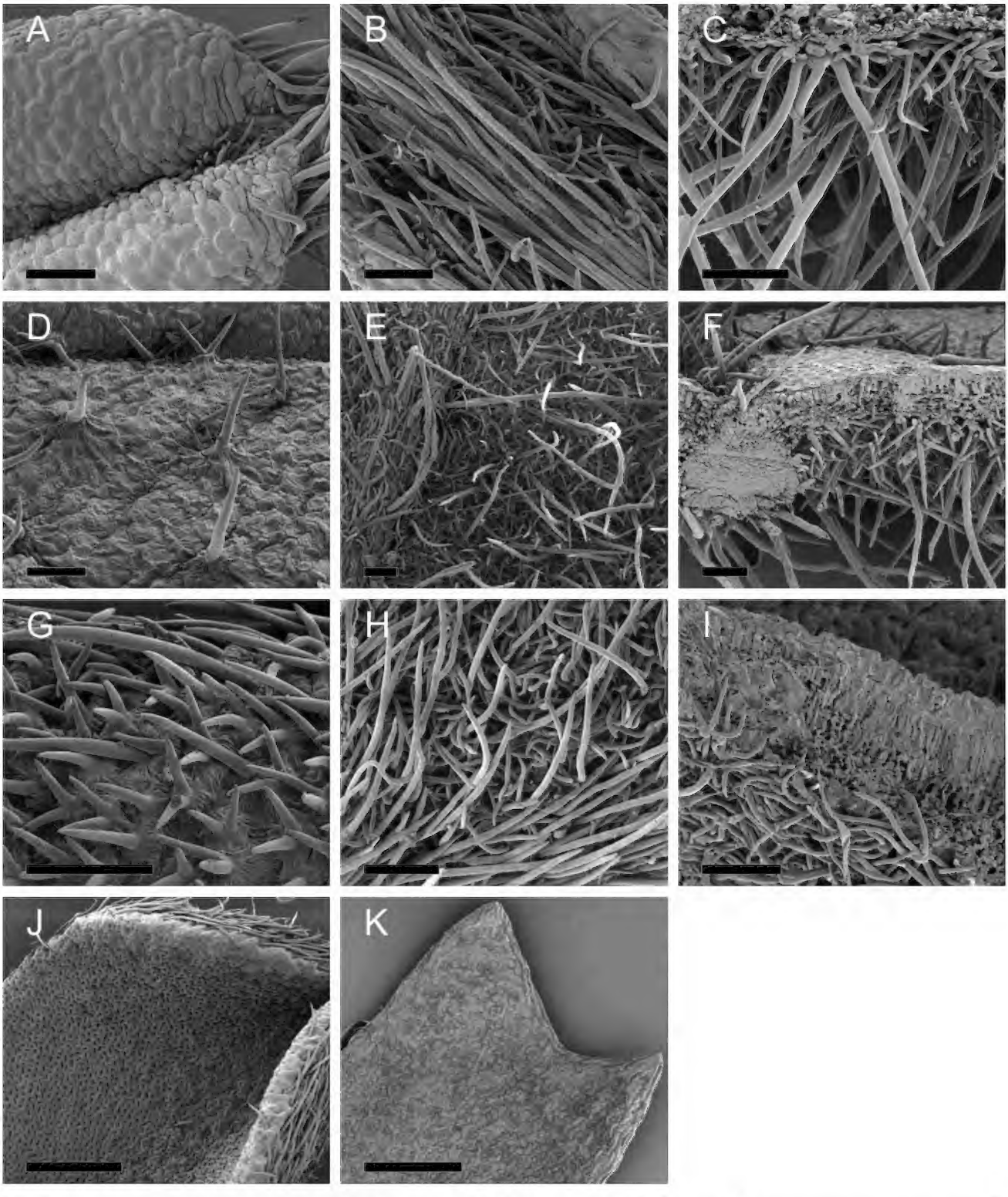

Fig. 7. Indumentum of leaves of *Trymalium*. **A–B** *T. ledifolium*; **C–F** *T. floribundum*; **G–J** *T. wayi*; **K** *T. monospermum*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**), cross section through leaf with upper leaf surface on top of the image. Scale A–I = 100 µm; J–K = 500 µm.

Pomaderris brevifolia (Fig. 8J–L)

Upper surface: Glabrous, surface with irregular wrinkles. Midrib with simple or bifid trichomes (50–100 µm long).

Lower surface: Silky indumentum of 200–300 µm long antrorse bifid hairs overlaying smaller 4-armed fasciculate and 4–8-armed appressed stellate hairs (with rays c. 50 µm long).

Pomaderris clivicola (data from Ross 1990)

Upper surface: Densely velvety indumentum of appressed stellate trichomes c. 100 µm long (possibly fasciculate trichomes with 4–5 rays).

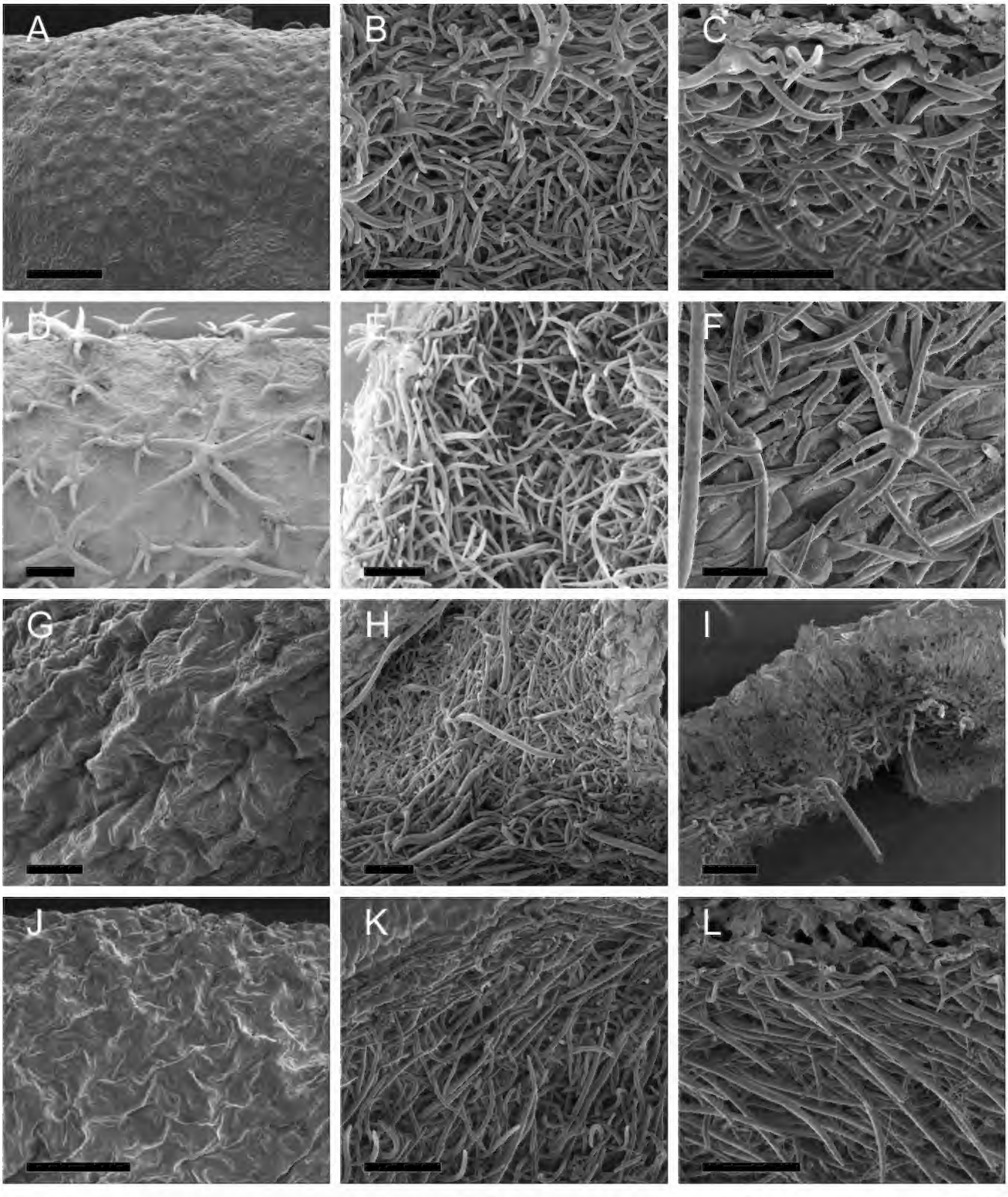

Fig. 8. Indumentum of leaves of *Pomaderris*. **A–C** *P. elliptica*; **D–E** *P. angustifolia*; **F–I** *P. obcordata*; **J–L** *P. brevifolia*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**) & **F**, lower surface; **C**, **I**, **L** cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm.

Lower surface: Densely pubescent with c. 200 µm long curved appressed stellate trichomes (possibly fasciculate with 8–10 rays) overlain by straight simple hairs (500–700 µm long).

Pomaderris elliptica (Fig. 8A–C)

Upper surface: Glabrous, pitted in the sunken centre of each epidermal cell.

Lower surface: Very densely tomentose to felted indumentum of intertwined appressed stellate trichomes with 6–8 rays (rays c. 100 µm long) and sometimed very sparse c. 100 µm long simple hairs. Midrib with 6–8-armed multiradiate hairs (rays 100–200 µm long).

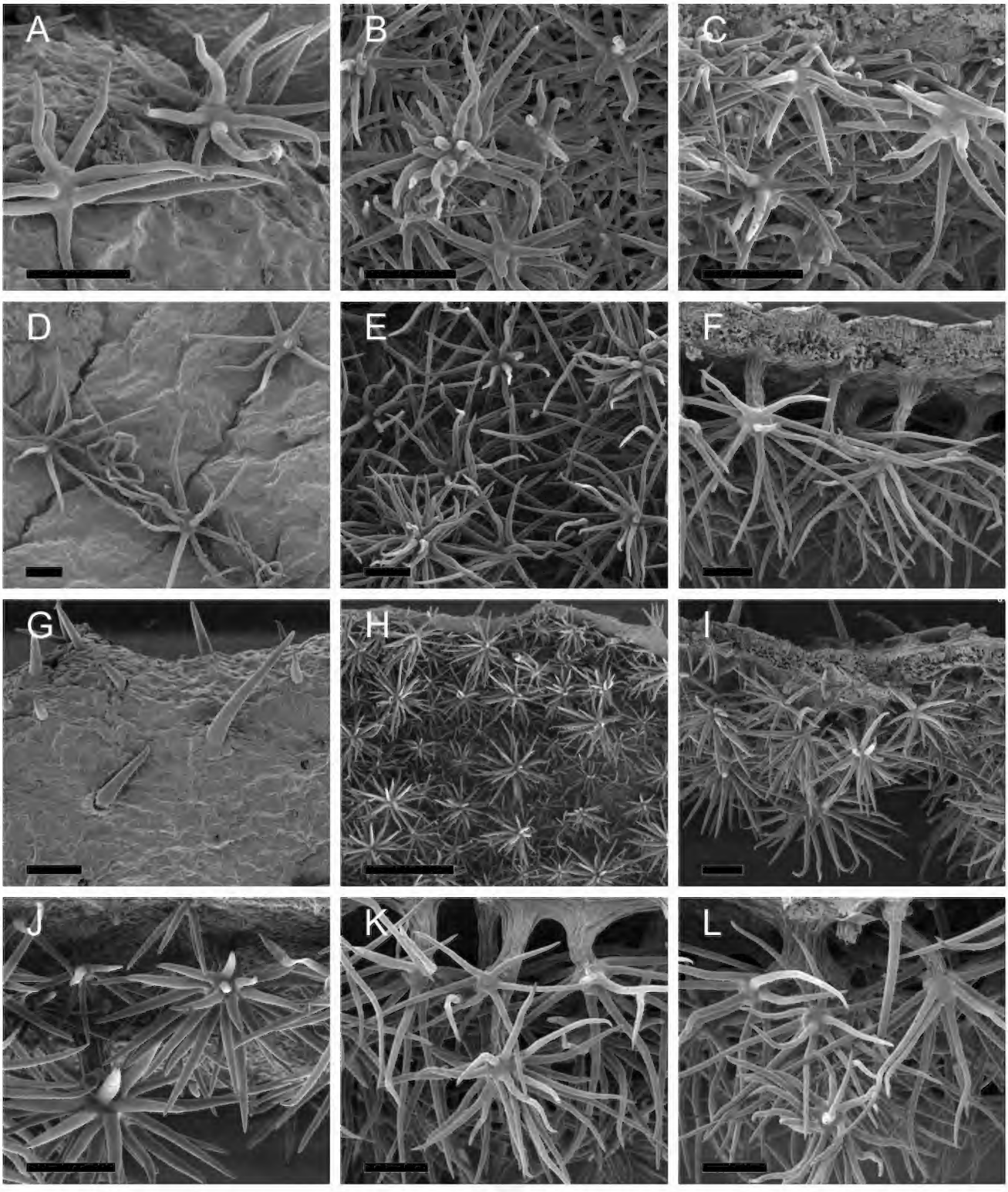

Fig. 9. Indumentum of leaves of *Pomaderris*. **A–C** *P. apetala*; **D–F**, **K**, **L** *P. aspera*; **G–J** *P. racemosa*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale A–G, I–L = 100 µm; H = 500 µm.

Pomaderris lanigera (data from Ross 1990, who illustrated two variants)

Upper surface: Moderately densely pubescent with straight simple trichomes, 250–500 µm long.

Lower surface: Densely pubescent with appressed stellate hairs (arms c. 300 µm long) overlain by straight to curly 500–1000 (–2000) µm long simple hairs.

Pomaderris obcordata (Fig. 8F–I)

Upper surface: Glabrous, surface folded and parallel striate [but flat or nearly so in vivo; N.G. Walsh, pers. comm., May 2020]. Midrib with 4–8-armed appressed stellate trichomes (rays c. 100 µm long).

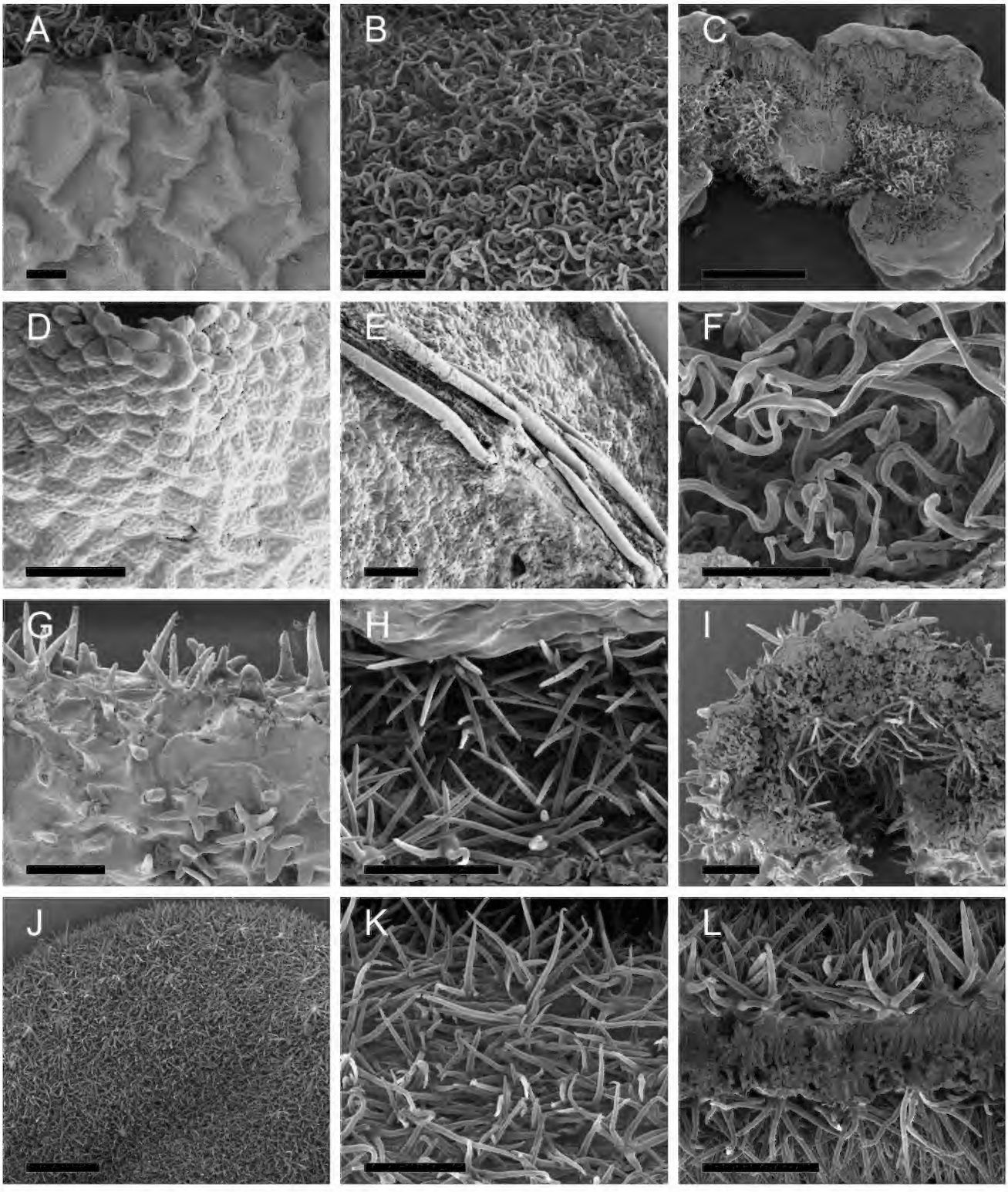

Fig. 10. Indumentum of leaves of *Siegfriedia* and *Cryptandra*. **A–C**, **F** *Si. darwinioides*; **D–E** *C. amara*; **G–I** *C. intermedia*; **J–L** *C. intratropica*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf (**L**, upper leaf surface on top of the image). Scale A–B, D–I, K–L = 100 µm; C, J = 500 µm.

Lower surface: Densely felted indumentum of 4–8-armed appressed stellate hairs, some umbonate (rays 100–150 µm long); midrib and secondary veins with sparse appressed stellate hairs and c. 400 µm long simple hairs.

Pomaderris prunifolia (data from Ross 1990)

Upper surface: Scabrous with stout simple (rarely divided) trichomes, 300–500 µm long [the surface may be also glabrous; Walsh 1999].

Lower surface: Densely pubescent with appressed stellate (possibly multiradiate) trichomes with rays c. 300–400 µm long and dendroid multiradiate trichomes (rays 400–500 µm long), especially on veins and midrib.

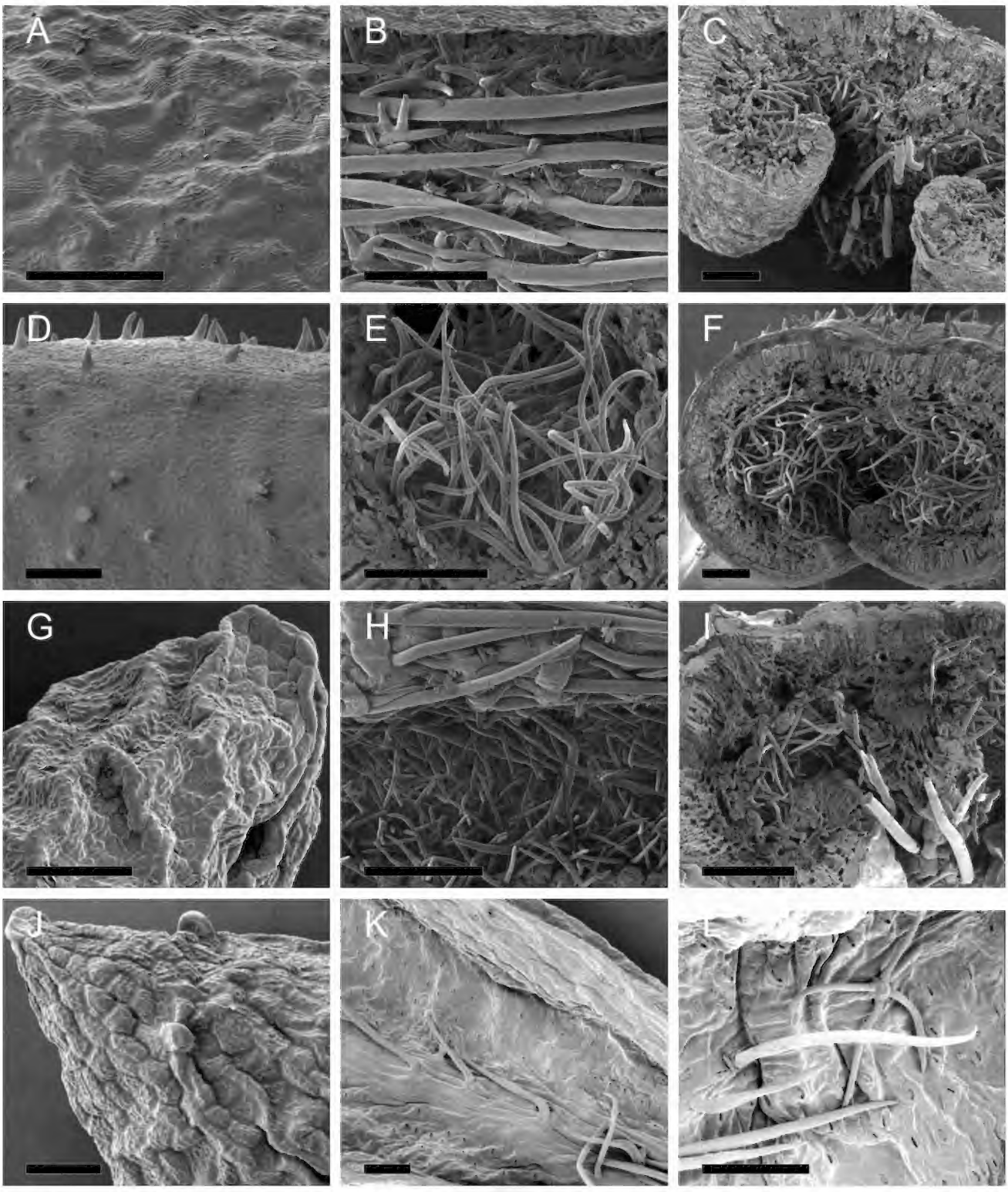

Fig. 11. Indumentum of leaves of *Cryptandra*. **A–C** *C. lanosiflora*; **D–F** *C. dielsii*; **G–I** *C. connata*; **J–L** *C. mutila*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**) & **L**, lower surface; **C**, **F**, **I**, cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm.

Pomaderris racemosa (Fig. 9G–J)

Upper surface: Sparsely tomentose to hirsute with 100–200 µm long simple hairs that easily break off and leave the base of the trichome behind. Surface smooth to slightly wrinkled with some ridges radiating from the base of the trichomes [the surface may also be glabrous; Walsh 1999].

Lower surface: Indumentum of two layers of stalked trichomes (appearing floccose): tall stalked multiradiate hairs with 6–30 rays (rays c. 200 µm long) and umbonate stalked to sessile appressed stellate hairs with 4–6 rays (each ray 50–100 µm long). These trichomes overlay long simple hairs (up to 100 µm) and 3–4-armed fasciculate hairs (rays c. 70 µm long).

Pomaderris tropica (data from Ross 1990)

Upper surface: Densely velvety indumentum of appressed stellate trichomes, rays c. 100 µm long (possibly fasciculate with 3–4 arms).

Lower surface: Densely pubescent with (possibly 8–10-armed) appressed stellate trichomes (each ray c. 200–300 µm long), overlain by appressed, straight simple hairs, 500–700 µm long.

Pomaderris vellea (data from Ross 1990)

Upper surface: Densely velvety with straight simple hairs, c. 200 µm long, occasionally the trichomes are basally divided.

Lower surface: Densely pubescent with curly simple hairs, c. 500–600 µm long [these almost certainly overlay stellate hairs, similar to the closely related *Pom. lanigera* (above); N.G. Walsh, pers. comm., May 2020].

Serichonus gracilipes (Fig. 6A–C)

Upper surface: Sparsely pubescent with c. 200 µm long erect simple hairs. The leaf surface is deeply wrinkled throughout.

Lower surface: Densely pubescent to villose indumentum of c. 400 µm long wavy simple hairs overlaying appressed stellate hairs with a distinct umbo, with 4–6 rays (each 100–200 µm long).

Siegfriedia darwinioides (Fig. 10A–C, F)

Upper surface: Glabrous, deeply folded, epidermis with a striate surface pattern.

Lower surface: Densely felted and matted indumentum of 2- to possibly 4-armed very long and curly fasciculate hairs (rays at least 200–500 µm long). Exact measurements were impossible due to the matted nature of the indumentum.

Spyridium burragorang (Fig. 4G–I, L)

Upper surface: Glabrous, surface irregular striate. Floral leaf with a densely felted indumentum of intertwined, slightly curly 6–8-armed multiradiate hairs (rays c. 100 µm long) and 200–300 µm long interspersed simple hairs.

Lower surface: Densely felted indumentum of intertwined curly 6–8-armed multiradiate hairs (rays 100–150 µm long) and up to 1000 µm long simple hairs on midrib and margins.

Spyridium daltonii * (Fig. 5A–C)

Upper surface: Glabrous, densely papillose to verrucose, with a somewhat striate pattern of ridges emanating from the centre of each wart-like protuberance.

Lower surface: Densely felted indumentum of stellate trichomes with rays c. 50–150 µm long (the exact type of hair was not observed with SEM), interspersed long simple hairs, 200–400 µm long. Midrib with long antrorse simple trichomes (400–600 µm long) and (2–)3–6-armed antrorse comb-like appressed stellate hairs (rays 100–200 µm long).

Spyridium furculentum * (Fig. 4J–K)

Foliar trichomes of this species are all stalked multiradiate hairs with (4–) 6–10 rays, which are placed on a broad multicellular pedestal.

Upper surface: Glabrous, except for some sparsely scattered trichomes (rays c. 150 µm in length). Floral leaves not examined.

Lower surface: Sparse to medium dense cover of trichomes (rays c. 200 µm long) on lower lamina and midrib.

Spyridium globulosum (Fig. 4A–B)

Upper surface: Glabrous, surface ± smooth. Midrib with 60–80 µm long simple hairs. Floral leaves not examined with SEM.

Lower surface: Densely felted indumentum of entangled multiradiate hairs with 6–8 rays (rays c. 100 µm long). Midrib less hairy, with smaller 4–8-armed appressed stellate hairs (arms 50–100 µm long) and long simple hairs, 500–1000 µm long.

Spyridium parvifolium (Fig. 4C–F)

Upper surface: Sparsely pubescent to hispid indumentum of simple hairs on a pedestal, 150–500 µm long. Surface irregularly striate. Floral leaves have additionally a very dense felted indumentum of entangled multiradiate hairs with 6–8 rays (rays c. 150 µm long).

Lower surface: Very dense, felted to pubescent indumentum of (6–) 8 (–10)-armed multiradiate trichomes (rays 150–200 µm long) with interspersed very long simple hairs (c. 1000 µm long), which are denser on midrib and leaf margin.

Stenanthemum centrale (Fig. 5G–I)

Upper surface: Densely tomentose indumentum of 2–4-armed fasciculate hairs with pedestal (rays 150–200 µm long) and interspersed simple hairs of the same length.

Lower surface: A dense indumentum of silky antrorse long simple hairs, 500–600 µm in length, overlying intertwined 4-armed multiradiate hairs of medium density (rays c. 150 µm in length).

Stenanthemum leucophractum * (Fig. 5D–F)

Upper surface: Densely papillate; the papillae may develop into the pedestals of fasciculate hairs, if rays develop. Sparsely tomentose with fasciculate hairs, 2–4 rays (each ray c. 100 µm long) and interspersed simple hairs 150–250 µm long.

Lower surface: Villous to silky indumentum of more than 500 µm long simple hairs. Possibly appressed stellate hairs below, but not visible on SEM images.

Trymalium ledifolium* var. *rosmarinifolium * (Fig. 7A–B)

Upper surface: Glabrous, epidermis parallel-striate. Midrib with 50–100 µm long trichomes; type of hair not visible on SEM.

Lower surface: Densely tomentose to felted indumentum of possibly multiradiate hairs (rays 100–200 µm long) and 200–500 µm long simple hairs. Midrib moderately covered with 4–8-armed appressed, sometimes umbonate stellate hairs (rays 50–100 µm long), and 200–500 µm long simple antrorse hairs.

Trymalium monospermum (Fig. 7K)

Upper and lower surface: Completely glabrous, surface wrinkled. Epidermis covered with a glaucous thick layer of wax.

Trymalium odoratissimum* subsp. *trifidum (Fig. 7C–F)

Upper surface: Sparsely pubescent indumentum of 200–400 µm long simple hairs. Midrib with V-shaped bifid fasciculate hairs, with rarely up to 4 rays (rays 100–400 µm long) [becoming glabrous with age and usually described as such; Rye 1995b]. Epidermis parallel-striate.

Lower surface: Densely tomentose to felted indumentum of 4–8-armed multiradiate trichomes (rays c. 400 µm long) and 500–1000 µm long simple hairs. Midrib moderately covered with 4–9-armed appressed umbonate stellate hairs (rays 100–150 µm long) and simple hairs that are slightly longer than the ones on the lamina (c. 1000 µm).

Trymalium wayi (Fig. 7G–J)

Upper surface: Young leaves moderately to densely tomentose with simple and V-shaped bifid fasciculate hairs, with rarely up to 4 rays (rays c. 50 µm long), becoming glabrous with age, hairs in older leaves only persisting on midrib. Surface deeply wrinkled and grooved. Epidermis parallel-striate.

Lower surface: Moderately dense silky indumentum of 400–500 µm long simple hairs overlaying very dense entangled 4–6 (–8)-armed appressed stellate hairs with umbo (rays 50–150 µm long). Simple hairs denser at midrib.

General observations

Simple hairs

Simple hairs were found on leaves of all examined species, except *Cryptandra intratropica*, *Pomaderris apetala* and *Trymalium monospermum*. It is possible to divide these simple hairs into two categories: erect and appressed hairs.

Erect hairs can be small, persistent and up to 100 µm long, as observed on the upper surface of *Cryptandra dielsii* (Fig. 11D) and *C. intermedia* (Fig. 10G). Tall erect hairs are c. 100–400 µm long on the upper surface and up to 1000 µm long on the lower surface of the leaf. In many species they were found on both surfaces. Frequently, they wear off on the upper surface with age and only persist in the impressed midrib. For example in *Stenanthemum gracilipes* (Fig. 6A, C), or in *Pomaderris racemosa* (Fig. 9G), scars of broken-off trichomes can be observed. On both, the upper and the lower surface, erect simple hairs occur interspersed with stellate trichomes (e.g. Figs 4F, 7F, 9L). In three species, the erect simple hairs had a distinctly raised base (pedestal): *Pom. aspera* (Fig. 9F), *Spyridium parvifolium* and *Polianthion collinum*.

Appressed hairs are mostly antrorse and 200–1200 µm long, in some cases they are up to 2000 µm long. They arise only on the lower surface and are usually conspicuous on the midrib (e.g. Figs 4B, 10E, 11B), secondary veins (if present) and leaf margins (e.g. Figs 5D, 6G). They may also be interspersed with stellate trichomes on the leaf lamina (Fig. 8K) or produce a dense villous or silky indumentum overlaying smaller stellate trichomes (e.g. Figs 7F, 8H).

Some simple hairs have a slightly wavy or curly appearance (e.g. Figs 5C, 8B). In *Stenanthemum leucophractum* (Fig. 5E) and *Cryptandra intermedia* (Fig. 10G) there appears to be a gradient from simple to bifid and stellate trichomes.

Papillae

Different kinds of papillae were observed on the upper surface of leaves. In *Cryptandra intermedia* (Fig. 10G) and *C. mutila* (Fig. 11J), papillae were round emergences, scattered on the upper surface. *Spyridium daltonii* had dense conical papillae that were marked with a distinctly striate surface pattern (Fig. 5B). In one species, *Stenanthemum leucophractum*, it appeared that the papillae were actually the pedestals of fasciculate hairs that failed to develop rays (Fig. 5D, E). As such there seemed to be a gradient from papillae to pedestals with rudimentary rays and then to fully developed fasciculate hairs.

Stellate trichomes

The presence of stellate trichomes is confirmed as a synapomorphy of the tribe Pomaderreae (Richardson *et al.* 2000b; Medan and Schirarend 2004). Three types of stellate trichomes were distinguished in this study: stellate, fasciculate, and multiradiate hairs. They could be found on leaves of all species, except *Cryptandra amara* and *Trymalium monospermum*. In *C. amara*, stellate trichomes are present on other parts of the plant, such as stems and flowers, whereas *T. monospermum* is the only species in Pomaderreae to be completely glabrous throughout (Rye 2000). Herzog (1903) reported fasciculate hairs on some species of *Rhamnus* L. (tribe Rhamneae), but Johnston & Johnston (1987) commented that these were just closely spaced simple hairs. Specialised two-armed hairs occur in *Sageretia* Brongn. (Johnston 1974 labelled them "medifixed hairs"; Medan and Schirarend 2004), but these were not observed in Pomaderreae.

Table 4. Indumentum cover of the lower surface of leaves of Pomaderreae as observed with SEM. Results from Ross (1990) are shaded in grey. The length of simple hairs or the rays of stellate hairs is designated by diamonds: ♦, < 50 µm; ♦♦, 50–150 µm; ♦♦♦, 150–250 µm; ♦♦♦♦, 250–400 µm; ♦♦♦♦♦, 400–800 µm; ♦♦♦♦♦♦, 800–1200 µm. The number of rays per stellate hair is indicated. Appr., appressed; D, dendroid trichome; M, hairs only on midrib; P, trichome with pedestal; W, wavy or curly hair. An asterisk after the species name indicates that only limited information was available from SEM.

Taxon	Indumentum	Simple	Fasciculate	Appr. stellate + umbo	Appr. stellate	Multiradiate	Multiradiate + stalk
Polianthion wichurae	medium-dense tomentose					♦♦♦ 8–10	
Pol. bilocularis	dense tomentose to felted	♦♦♦♦♦ W			♦♦ 6–8 (–10)	♦♦♦ 8–10	
Pol. minutiflorum	dense tomentose	♦♦, M ♦♦♦♦			♦♦ 4–8	♦♦♦ 4–8	
Pol. collinum	dense tomentose (-velvety)	♦♦♦♦			♦♦ 4		
Spyridium globulosum	dense felted	M ♦♦♦♦♦			M ♦♦ 4–8	♦♦ 6–8	
Sp. parvifolium	felted-pubescent	♦♦♦♦♦♦				♦♦♦ (6–) 8 (–10)	
Sp. burragorang	dense felted	M ♦♦♦♦♦♦				♦♦ 6–8 W	
Sp. furculentum *	sparse-medium	(?)					♦♦♦ (4–) 6–10
Sp. daltonii	dense felted	♦♦, M ♦♦♦♦♦			M ♦♦ (2–) 3–6	♦♦ 2?–6?	
Stenanthemum leucophractum *	villous-silky	♦♦♦♦–♦♦♦♦♦				(?)	
St. centrale	silky strigose	♦♦♦♦♦				♦♦♦ 4	
Serichonus gracilipes	dense pubescent to villose	♦♦♦♦ W		♦♦–♦♦♦ 4–6			
Papistylus grandiflorus	dense sliky (to villose)	♦♦♦♦		♦♦♦ (4–)6			
Blackallia nudiflora	silky (to villose)	♦♦♦♦	♦♦ 2		♦♦ 3–6		
Trymalium ledifolium *	dense tomentose-felted	♦♦♦–♦♦♦♦		M ♦♦ 4–8		♦♦–♦♦♦	
T. floribundum	dense tomentose-felted	♦♦♦♦♦♦		M ♦♦ 4–9		♦♦♦♦ 4–8	
T. wayi	moderate-dense silky	♦♦♦♦♦		♦♦ 4–6 (-8)			
T. monospermum	glabrous, glaucous						
Pomaderris angustifolia *	dense felted	(?)	♦♦ 6–8			♦♦♦ 4–8	
Pom. elliptica	dense tomentose-felted	♦♦	♦♦ 6–8			M ♦♦–♦♦♦ 6–8	
Pom. apetala	dense felted		♦♦ 6–8				♦♦–♦♦♦ 10–20 (–25) D?
Pom. aspera	dense felted (floccose)	♦♦♦ P					♦♦♦ (6–) 10–40 D
Pom. racemosa	floccose	♦♦	♦♦ 3–4	♦♦ 4–6 S			♦♦♦ 6–30
Pom. clivicola	dense pubescent	♦♦♦♦♦				♦♦♦ 6–8	
Pom. prunifolia	dense pubescent		?			♦♦♦ 10	♦♦♦♦ 12
Pom. lanigera form 1	dense pubescent	♦♦♦♦♦–♦♦♦♦♦♦ W	♦♦♦♦ 4				
Pom. lanigera form 4	dense pubescent	♦♦♦♦♦–♦♦♦♦♦♦	♦♦♦♦ 4				
Pom. vellea	dense pubescent	♦♦♦♦♦ W					
Pom. tropica	dense pubescent	♦♦♦♦♦	♦♦♦–♦♦♦♦ 8–10				
Pom. obcordata	dense felted	M ♦♦♦♦♦		♦♦ 4-8	♦♦ 4–8		
Pom. brevifolia	silky		♦♦♦♦ 2, ♦♦ 4		♦♦ 4–8		
Siegfriedia darwinioides	dense felted-matted	(?)	♦♦♦–♦♦♦♦♦ 2 W				
Cryptandra amara	glabrous, M strigose	M ♦♦♦♦♦					
C. intratropica	dense tomentose	M ♦♦♦–♦♦♦♦				♦♦ 7–10	
C. intermedia	moderate to dense tomentose				♦♦ 6–8	♦♦ 6–8	
C. mutila	glabrous, M strigose	♦♦♦♦♦		♦♦ 4 (rare)			
C. lanosiflora	dense tomentose	M ♦♦♦♦♦	♦–♦♦ 5–10		M ♦–♦♦ 5–10		
C. dielsii	moderate-dense tomentose	(?)				♦♦♦ 5–6	
C. connata	dense tomentose	M ♦♦♦♦	♦♦ 2–4		M ♦♦ 2–4	♦♦ 5–8	

Table 5. Indumentum cover of the upper surface of leaves of Pomaderreae as observed with SEM. Results from Ross (1990) are shaded in grey. The indumentum of floral leaves is reported in square brackets. The length of simple hairs or the rays of stellate hairs is designated by diamonds: ♦, < 50 µm; ♦♦, 50–150 µm; ♦♦♦, 150–250 µm; ♦♦♦♦, 250–400 µm; ♦♦♦♦♦, 400–800 µm; ♦♦♦♦♦♦, 800–1200 µm. The number of rays per stellate hair is indicated. Appr., appressed; M, hairs only on midrib; P, trichome with pedestal; W, wavy or curly hair. An asterisk after the species name indicates that only limited information was available from SEM.

Taxon	Indumentum	Papillae	Simple	Fasciculate	Appr. stellate	Multiradiate
Polianthion wichurae	dense tomentose-felted		♦♦	♦♦ (5–) 8 (–10) P		
Pol. bilocularis	dense tomentose				♦♦ 5-8 (–10)	♦♦♦ 8–10
Pol. minutiflorum	dense tomentose		♦	♦ 2–6		
Pol. collinum	dense tomentose		♦ P	♦ 2–4 (-8) P		
Spyridium globulosum	glabrous		♦♦			
Sp. parvifolium	sparse pubescent-hispid [dense felted, intertwined]		♦♦♦–♦♦♦♦♦ P			[♦♦♦ 6–8 W]
Sp. burragorang	glabrous [dense felted, intertwined]		[♦♦♦]			[♦♦ 6–8 W]
Sp. furculentum *	scattered					♦♦–♦♦♦ (4–) 6–10
Sp. daltonii	glabrous					
Stenanthemum leucophractum *	tomentose	dense	♦♦♦	♦♦ 2–4 P		
St. centrale	dense tomentose		♦♦♦	♦♦♦ 2–4 P		
Serichonus gracilipes	sparse pubescent		♦♦♦			
Papistylus grandiflorus	glabrous, some on M		♦♦ rare			
Blackallia nudiflora	glabrous					
Trymalium ledifolium *	glabrous			M ♦–♦♦ ?		
T. floribundum	sparse pubescent		♦♦♦–♦♦♦♦	M ♦♦–♦♦♦♦ 2 (–4)		
T. wayi	moderate-dense tomentose			♦♦ 2 (–4)		
T. monospermum	glabrous (glaucous)					
Pomaderris angustifolia *	scattered			♦♦ 2–4	♦♦♦ 4–8	
Pom. elliptica	glabrous					
Pom. apetala	scattered					♦♦♦ 10–20
Pom. aspera	scattered					
Pom. racemosa	sparse tomentose-hirsute		♦♦–♦♦♦			
Pom. clivicola	dense velvety			♦♦ 4–5		
Pom. prunifolia	scattered, scabrous		♦♦♦♦			
Pom. lanigera form 1	moderate pubescent		♦♦♦♦–♦♦♦♦♦			
Pom. lanigera form 4	moderate pubescent		♦♦♦			
Pom. vellea	dense velvety		♦♦	♦♦ 2 rare		
Pom. tropica	dense velvety			♦♦ 3–4		
Pom. obcordata	glabrous					
Pom. brevifolia	glabrous M only			♦♦ 1–2		
Siegfriedia darwinioides	glabrous					
Cryptandra amara	glabrous					
C. intratropica	dense tomentose					♦♦ (3–) 4–10
C. intermedia	papillose	moderate-dense	♦♦	♦♦ 4–6		??
C. mutila	papillose	sparse				
C. lanosiflora	glabrous					
C. dielsii	tomentose-hispid		♦			
C. connata	glabrous					

Table 6. Surface sculpturing on the upper surface of leaves of Pomaderreae as observed with SEM. Due to trichome cover on the surface, the surface could not be examined in *Polianthion*, *Stenanthemum* and *Cryptandra intratropica*. An asterisk after the species name indicates that only limited information was available from SEM. Abbreviation: +, presence of type of sculpturing; ?, questionable presence.

Taxon	Wrinkled	Irregular striate	Parallel striate	Punctate	Punctate centre of cells
Spyridium globulosum	+				
Sp. parvifolium		+			
Sp. burragorang		+			
Sp. furculentum *		?			
Sp. daltonii		+			
Serichonus gracilipes	+				
Papistylus grandiflorus	+				
Blackallia nudiflora	+				
Trymalium ledifolium *			+		
T. floribundum			+		
T. wayi			+		
T. monospermum					
Pomaderris angustifolia *		possibly	possibly		
Pom. elliptica					+
Pom. apetala		+			
Pom. aspera		+			
Pom. racemosa		+	possibly radiating from hair base		
Pom. obcordata			+		
Pom. brevifolia		+	+		
Siegfriedia darwinioides		+	+		
Cryptandra amara				+	
C. intermedia				+	
C. mutila				+	
C. lanosiflora			+		
C. dielsii				+	
C. connata				+	

Gemoll (1902) did not distinguish different stellate trichomes, but listed them all under his type IA (Table 2). He reported stellate trichomes with a long multicelled stalk (type IIB) in some species of *Pomaderris*, and with a short multicelled stem (type IA) on the upper surface of *Pom. aspera*. This type IA is possibly a reduced version of type IIB, since in *Pom. aspera* the actual heads of the multiradiate hairs do not differ, only the length of the stalk (Fig. 9D, F). *Spyridium coactilifolium* Reissek, for which Gemoll reports a unique type of trichome (type IIA), was not examined in this study. Similarly, Ross (1990) only distinguishes between sessile and stalked stellate trichomes. The results of these studies are confirmed here with SEM.

Fasciculate hairs were found on nearly all species of *Trymalium*, *Siegfriedia*, *Pomaderris*, *Blackallia*, some species of *Cryptandra* and *Stenanthemum*, and *Polianthion collinum*. The number of rays per hair and the size and shape of fasciculate hairs were variable and ranged from bifid hairs to hairs with 10 rays, but usually 2–8 rays were present. The hairs were mainly observed on the lower surface of the leaf, but in *Trymalium* (e.g. Fig. 7G), *St. leucophractum* (Fig. 5D, E) and *St. centrale* (Fig. 5G, I) they were exclusively found on the upper surface.

Appressed stellate hairs were usually found in combination with other trichomes. They were present as a bottom layer of trichomes in a multi-layered indumentum, and often hidden by the overlaying trichomes. Only in two of the studied species, *Polianthion bilocularis* (Fig. 3D, E) and *Pomaderris angustifolia* (Fig. 8D), appressed stellate hairs were recorded on the upper surface. In 17 other species examined with SEM (Tables 4, 5), appressed stellate trichomes were found on the lower surface; in six of these species only on the midrib and veins. Umbonate appressed stellate hairs were seen on nine of the examined species, including all species of *Trymalium* examined, *Serichonus gracilipes*, *Papistylus grandiflorus*, *Pomaderris obcordata*, *Pom. racemosa* and *Cryptandra mutila*.

Multiradiate trichomes were among the most common trichomes observed, and are usually part of the indumentum of the lower surface of the leaf. Four species were observed to always have multiradiate hairs on the upper surface: *Polianthion bilocularis*, *Pomaderris apetala*, *Pom. aspera* and *Cryptandra intratropica*. Additionally, the floral leaves observed in *Spyridium parvifolium* and *Sp. burragorang* also carried multiradiate hairs on the upper surface. In Pomaderreae, multiradiate trichomes have 4–20 rays. ***Stalked multiradiate trichomes*** were detected on only three species: *Pom. aspera*, *Pom. apetala* and *Pom. racemosa* (Fig. 9). They are identical with Gemoll's type IIB that he reported for *Pom. apetala* (Gemoll 1902) and had multiradiate 'heads' crowded with (6–) 10–40 rays per head. In *Pom. aspera* and possibly *Pom. apetala* the multiradiate trichomes are dendroid with up to three 'heads' (Fig. 9K, L).

Spyridium furculentum has a different kind of stalked multiradiate hair. It has 6–10 rays on a not very well developed 'head' and sits on a broad multicellular base (Fig. 4K). This type of hair is possibly similar to the trichomes of type IIA, reported by Gemoll (1902) for *Sp. coactilifolium*, since the two species are closely related (Kellermann & Barker 2012).

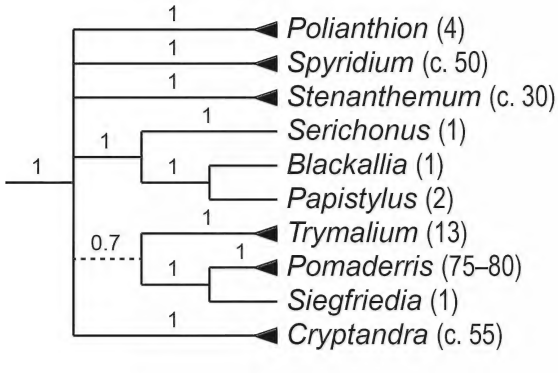

Fig. 12. Summary phylogeny of Pomaderreae, abridged from the Bayesian analysis of the family by Hauenschild *et al.* (2018), using molecular data from 15 DNA regions. Posterior probability is indicated above branches. Nodes with support below 0.7 are collapsed; support below 1 is indicated by a dashed line. Triangles show that more than one taxon was used for the analysis. Species numbers for each genus are indicated in brackets.

Surface sculpturing

The sculpturing on the upper epidermis could not be examined in species with a dense indumentum on the upper surface, i.e. it was not recorded for seven of the 32 examined species (Table 5).

The surface had a distinctly ***wrinkled*** appearance in *Blackallia nudiflora*, *Spyridium globulosum*, *Serichonus gracilipes* and *Papistylus grandiflorus* (Figs 4A, 6A, D, G). It was ***punctate*** in *Cryptandra amara*, *C. connata*, *C. dielsii*, *C. mutila* and possibly *C. intermedia* (Figs 10D, G, 11D, G, J). *Pomaderris elliptica* also displayed a punctate surface (Fig. 8A), however, the punctate surface of each epidermal cell was distinctly sunken, compared to the slightly raised or level surface in the other species. All remaining species had a ***striate*** surface pattern, which was parallel in three species of *Trymalium*, *Pom. obcordata* and possibly *Pom. brevifolia* (Figs 7A, D, G, 8G, J), and irregularly striate elsewhere.

Some of these wrinkles, folds and striations could also be an artefact of drying. However, this could not be ascertained, as fresh material was not available for comparison.

Trichome distribution in Pomaderreae

The distribution of trichomes in the tribe is discussed below, using the clades and genera resolved in phylogenies of the tribe (Kellermann *et al.* 2005; Ladiges *et al.* 2005) and most recent molecular analyses of the family (Hauenschild *et al.* 2016, 2018). A summary phylogeny of the tribe is depicted in Fig. 12.

Polianthion ('Bilocular Clade' of Kellermann *et al.* 2006; Fig. 3)

Characteristic for the four species of this genus is the densely tomentose indumentum of stellate trichomes on both surfaces of the leaf. The upper surface is covered by very short erect fasciculate hairs in *Polianthion minutiflorum* and *Pol. collinum*, and slightly longer ones in *Pol. wichurae*. These three species also have interspersed short simple hairs among the stellate trichomes. *Polianthion bilocularis* has a dense cover of entangled small appressed stellate and larger multiradiate hairs on the upper surface; the presence of simple hairs could not be ascertained. The lower surface of *Pol. wichurae* was covered only by multiradiate trichomes, whereas the other three species had a cover of appressed stellate, multiradiate and simple hairs. These simple hairs were up to 600 µm long in *Pol. bilocularis*. In *Pol. collinum* they were overlying the stellate indumentum of the lower surface, giving the leaf a velvety appearance. *Cryptandra intratropica* is the only other species examined with such a dense indumentum on both leaf surfaces. Its indumentum is similar to that

in species of *Polianthion* in density, but it only seems to consist of multiradiate trichomes. Due to the dense trichome cover, the epidermis could not be examined; in *Pol. wichurae* it is possibly wrinkled (Fig. 3C).

Spyridium (Fig. 4, 5A–C)

Species of *Spyridium* typically have a dense indumentum of stellate and simple trichomes on the lower surface of the leaf. The upper surface is glabrous or sparsely hairy; some species have floral leaves, which are covered with a dense white indumentum.

The upper surfaces of *Spyridium globulosum*, *Sp. burragorang* and *Sp. daltonii* are totally glabrous, the indumentum of *Sp. parvifolium* ranges from glabrous (Walsh 1999) to hispid (in the specimen examined; Fig. 4D, F) on the upper surface and *Sp. furculentum* has sparse stellate trichomes. In *Sp. globulosum* the epidermis has a wrinkled appearance, while in the remaining four species it appears irregularly striate (Fig. 4G). The upper surface of leaves of *Sp. daltonii* is densely covered in conical papillae. The indumentum of floral leaves was observed in *Sp. parvifolium* and *Sp. burragorang*. In both cases it consisted of very dense intertwined multiradiate and simple hairs with curly or spiralling rays (Fig. 4C, L).

The indumentum on the lower surface is composed of multiradiate hairs in all species examined. The distinct multiradiate hairs of *Spyridium furculentum*, which are located on a large base (as mentioned above), have also been reported in the related species *Sp. coactilifolium*, *Sp. coalitum* Kellermann & W.R.Barker, *Sp. fontis-woodii* Kellermann & W.R.Barker, *Sp. halmaturinum* (F.Muell.) F.Muell. ex Benth. and *Sp. scabridum* (Tate) Kellermann & W.R.Barker (Kellermann & Barker 2012). Appressed stellate hairs are visible on the midrib of *Sp. globulosum* and *Sp. daltonii*. Very long erect and spreading simple hairs (up to 1000 µm) were interspersed on the lower surface of *Sp. parvifolium*, becoming denser on the midrib and margins (Fig. 4E, F). The remaining species, except *Spyridium furculentum*, also had long simple hairs on the midrib of the lower surface; additional short simple hairs were found on *Sp. burragorang*.

Gemoll (1902) examined nine species of *Spyridium*, eight of which had stellate hairs of type IA on the lower surface (Table 2), only *Sp. coactilifolium* had trichomes of the unique type IIA.

Stenanthemum (Fig. 5D–I)

Two species of *Stenanthemum* (as defined in Rye 2001; Thiele 2007) were examined. The lower surface is covered in a characteristic densely silky-villous indumentum of long simple hairs, which are overlaying 4-armed multiradiate trichomes. The long simple hairs reach on to the upper surface along the margins. In *St. centrale*, the upper surface is covered with densely arranged erect 2- or 4-armed fasciculate hairs and occasional simple hairs. The upper surface of *St. leucophractum* appears densely papillose-tuberculate with occasional trichomes, however, close examination reveals that the papillae seem to be the bases of simple and fasciculate hairs that failed to develop rays (see above). Long simple hairs overlaying small stellate trichomes on the lower surface have been reported for most species of *Stenanthemum* (Rye 1995a, 2001; Thiele 2007) and seem to be characteristic for the genus.

Three small genera from Western Australia (Fig. 6)

Kellermann *et al.* (2007) described three closely related genera of Pomaderreae: *Blackallia*, *Serichonus* and *Papistylus*. Three species from these genera were examined in this study; the leaf morphology of these species is very similar.

The upper surface of the leaves is wrinkled. Young leaves of *Serichonus gracilipes* (Fig. 6A) and *Papistylus grandiflorus* (Fig. 6D) are moderately covered with simple hairs, which are erect and antrorse, respectively. Leaves become glabrous with age, except for a few hairs remaining at the midrib. *Blackallia nudiflora* (Fig. 6G) has a glabrous upper surface.

The lower surface in all three species is moderately covered with small appressed stellate hairs, which are umbonate in *Se. gracilipes* and *Pap. grandiflorus*; an umbo was not observed in *B. nudiflora*, but in addition, bifid fasciculate hairs were present in this species. These stellate trichomes are covered by a dense silky to villous layer of long antrorse simple hairs, which are straight and closely appressed in *Pap. grandiflorus* and *B. nudiflora*, but in *Se. gracilipes* they appear to be slightly undulating or wavy. The surface of the former two species becomes glabrous with age, whereas in *Se. gracilipes* the indumentum is persistent.

The indumentum on the leaves of these three species is very much alike and a close relationship of *Se. gracilipes*, *Pa. grandiflorus* and *B. nudiflora* can be confirmed from these observations. The hair cover is similar to species of *Stenanthemum*, however, in this genus the upper surface is not glabrous but densely papillose or tuberculate, with or without 2–4-fid trichomes; furthermore, the underlying layer of stellate trichomes on the lower surface is much denser.

Trymalium (Fig. 7)

Four species of *Trymalium* were examined with SEM. *Trymalium monospermum* (Fig. 7K) is an exception within Pomaderreae, as it is the only species that is totally glabrous on all parts of the plant. The leaf surfaces, however, are covered with a conspicuous glaucous layer of wax. As such, this species is not discussed in the following description of trichomes.

The upper surface of the leaves in the remaining species of *Trymalium* is glabrous or moderately to densely covered with erect simple or bifid fasciculate trichomes. With age, the upper surface tends to become glabrous

with only a few hairs remaining on the midrib (e.g. Fig. 7G, J). In leaves, which are otherwise glabrous on the upper surface (Fig. 7A), the midrib also carries hairs. The upper surface in *Trymalium ledifolium*, *T. odoratissimum* subsp. *trifidum* and *T. wayi* displays a parallel striate pattern; no surface sculpturing is discernible in *T. wayi*.

The lower surface has a densely tomentose to felted indumentum in *Trymalium ledifolium* (Fig. 7B, C) and *T. odoratissimum* (Fig. 7E, F), consisting of multiradiate hairs with long patent simple hairs. The midrib of these two species has appressed umbonate stellate hairs lying under long antrorse simple hairs.

The lower surface of *T. wayi* (Fig. 7H, I) consists of a layer of entangled umbonate appressed stellate hairs overlayed by long silky simple hairs. This type of indumentum is also found in *Stenanthemum* and might have developed due to similar selection pressures in these species, since molecular results, inflorescence, floral and fruit characters clearly place *T. wayi* in *Trymalium*. The difference in indumentum might, however, reflect the position of *T. wayi* as a geographically isolated taxon within the genus.

Pomaderris (Fig. 8–9)

With c. 75 species, *Pomaderris* is the largest genus of Pomaderreae. The results of SEM examinations of seven species were augmented with observations by Ross (1990) on five species of *Pomaderris* from Queensland. As can be expected in such a large genus, the indumentum varies quite considerably.

The upper surface of leaves in *Pomaderris* can be smooth and glabrous (*Pom. elliptica*, Fig. 8A), glabrous and wrinkled (*Pom. obcordata* and *Pom. brevifolia*, Fig. 8G, J), although this might be an artefact of drying of thicker leaved species (N.G. Walsh, pers. comm.). The upper indumentum consists of silky to hispid simple (Fig. 9G; Ross 1990) or stellate hairs (Fig. 8D; Ross 1990). The indumentum cover on the upper surface also varies within species, e.g. some forms of *Pom. prunifolia* may be glabrous (N.G. Walsh, pers. comm.) and not bear simple hairs as reported by Ross (1990: Fig. 1A). All species examined by SEM seem to have a parallel or irregularly striate surface pattern, with the exception of *Pom. elliptica*. In this species every epidermal cell is somewhat sunken in the middle and conspicuously punctate.

The indumentum on the lower surface contains both stellate and simple hairs, but five species had stellate hairs only (*Pomaderris apetala*, *Pom. brevifolia*, *Pom. clivicola*, *Pom. prunifolia* and *Pom. tropica*; the latter three not examined with SEM, data from Ross 1990). Simple hairs are very few and sparse in *Pom. elliptica* (see Walsh 1999); often this species is described as being devoid of simple hairs. *Pomaderris vellea* was reported by Ross (1990) to have only an indumentum of long curly simple hairs. However, the simple hairs in that species are extremely dense and completely obscure the underlying layer of stellate hairs (N.G. Walsh, pers. comm.). *Pomaderris brevifolia* appears to have long simple hairs on the lower surface, but these are actually bifid fasciculate hairs.

Walsh & Coates (1997) published an infrageneric classification for *Pomaderris*. Specimens from all but two of the seven sections, sect. *Flabellares* N.G. Walsh and sect. *Annulares* N.G. Walsh, were examined by SEM. Sect. *Biloculares* N.G. Walsh is now a synonym of *Polianthion* (Kellermann *et al.* 2006). Some of these sections, however, are not natural groups, but seem to be para- or polyphyletic assemblages (Kellermann *et al.* 2005; Chen *et al.* 2019). The indumentum characteristics of the lower surface of the leaves given by Walsh & Coates (1997) for the sections were confirmed by SEM in nearly all cases:

Sect. *Psilogyne* N.G.Walsh (represented by *Pomaderris angustifolia*) had a mixture of stellate and simple trichomes, concordant with their definition (Walsh & Coates 1997).

Sect. *Apetalae* N.G.Walsh (represented by *Pomaderris apetala* and *Pom. aspera*) is reported to have stellate trichomes only (Walsh & Coates 1997), but this was only the case in *Pom. apetala*. The lower surface of *Pom. aspera* also may have interspersed erect simple hairs (Fig. 9F, L), which are often not reported (e.g. Walsh 1999).

The largest section, sect. *Pomaderris*, accommodates species with a wide variety of indumenta. It is defined to have a trichome cover "of simple and stellate hairs (rarely stellate hairs only)" (Walsh & Coates 1997: 29). This is corroborated by SEM in *Pom. racemosa* and *Pom. elliptica*, and by the observations of Ross (1990) on *Pom. clivicola*, *Pom. lanigera*, *Pom. prunifolia* and *Pom. vellea*.

Sect. *Umbelliflorae* N.G.Walsh was represented in this study by two species, *Pomaderris brevifolia* from Western Australia and *Pom. obcordata* from southern Australia. Both species have a very similar indumentum of stellate and simple hairs, which agrees with the description of Walsh & Coates (1997), but molecular analyses do not place these two species as sister taxa (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Hauenschild *et al.* 2016, 2018). They are found in two geographically separated clades with species from Western Australia and south-eastern Australia.

Sect. *Flabellaris* is reported to have only a cover of stellate trichomes on the lower surface (Walsh 1990; Walsh & Coates 1997); no species from this section were examined with SEM.

Sect. *Annulares* is defined as having stellate and simple hairs on the lower surface of the leaves (Walsh & Coates 1997). This is confirmed by Ross (1990) in the description of *Pomaderris tropica*, but the illustration of

the lower surface (Ross 1990: Fig. 1E) does not show the simple trichomes reported for that species.

A striking feature of three species examined by SEM, *Pomaderris apetala*, *Pom. aspera* and *Pom. racemosa*, is the presence of stalked multiradiate and dendroid hairs with multiradiate 'heads' (Fig. 9) on the lower surface of the leaves. Gemoll (1902) observed trichomes of type IIB on *Pom. apetala*, *Pom. prunifolia* and *Pom. racemosa* (Table 2). Ross (1990) reports stalked trichomes for *Pom. prunifolia* and Moore (1986) lists stalked trichome types for *Pom. aspera*, *Pom. paniculosa* subsp. *novae-zelandiae* (L.B.Moore) N.G.Walsh, *Pom. edgerleyi* Hook.f. (as *Pom. prunifolia* var. *edgerleyi* (Hook.f.) L.B.Moore) and *Pom. rugosa* Cheeseman.

In *Pomaderris apetala* these hairs have short stalks and heads with 10–20 (–25) rays (Fig. 9C). The observation of "dense sessile stellate hairs" by Walsh (1999: 91) is probably due to the fact that the short stalks are hard to identify under a dissecting microscope. Long-stalked multiradiate hairs are found in *Pom. aspera* and *Pom. racemosa*, the heads of both species having more rays than *Pom. apetala*. Dendroid multiradiate hairs are recorded in *Pom. aspera* (Fig. 9K, L) with up to three 'heads' per trichome.

Walsh & Coates (1997) do not group these species with stalked or dendroid hairs together, but place *Pomaderris apetala*, *Pom. aspera*, *Pom. paniculosa* and *Pom. rugosa* into sect. *Apetalae*. *Pomaderris prunifolia*, *Pom. oraria* and *Pom. racemosa* are arranged in sect. *Pomaderris*. This corresponds with an indumentum of sparse multiradiate hairs on the upper leaf surface of the species placed into sect. *Apetalae* and the presence of simple trichomes on species from sect. *Pomaderris* (Fig. 9G; Walsh 1999). The molecular analyses (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Hauenschild *et al.* 2016, 2018) only included three of these taxa, *Pom. oraria*, *Pom. edgerleyi* and *Pom. rugosa*; resolution within *Pomaderris* was limited. Whether the stalked and dendroid trichomes have arisen twice independently or only once, should be the subject of future research.

Siegfriedia (Fig. 10A–C, F)

Sister taxon to *Pomaderris* is the monotypic genus *Siegfriedia* (Kellermann *et al.* 2005; Hauenschild *et al.* 2016, 2018). The upper leaf surface of *Si. darwinioides* is glabrous with deep folds (Fig. 10A); the epidermis displays a strigose pattern. The lower surface of the species is covered in a very dense, intertwined, often felted and matted indumentum of long curly bifid and four-armed fasciculate hairs that fill the cavity within the revolute leaf (Fig. 10B, C, F).

The indumentum of *Siegfriedia* is unique in Pomaderreae, and has not been observed in any other species. Although flower and fruit morphology, as well as the molecular results indicate a close relationship of *Pomaderris* and *Siegfriedia*, this cannot be ascertained from this survey of leaf trichomes. *Siegfriedia darwinioides* is very distinctive in many vegetative and floral characteristics, indumentum being only one of many (Rye 1996).

Cryptandra (Fig. 10C–L, 11)

Seven species were examined of *Cryptandra*. *Cryptandra connata*, previously included in the genus *Blackallia*, displayed indumentum characteristics comparable to other species of *Cryptandra*. This is confirmed by the results of molecular analysis (Kellermann *et al.* 2005; Hauenschild *et al.* 2016, 2018).

The upper surface for all except one of the species examined, *Cryptandra intratropica*, is typically glabrous or sparsely pubescent. *Cryptandra amara*, *C. connata* and *C. lanosiflora* have a totally glabrous surface. Some papillae are found on *C. mutila* (Fig. 11J) and *C. dielsii* has a cover of sparse hispid erect simple hairs (Fig. 11D). *Cryptandra intermedia* has a moderate to dense indumentum of simple and fasciculate hairs on the upper surface. The indumentum of *C. intratropica* only consists of dense multiradiate hairs. The irregular nature of these trichomes (in regards to ray length and thickness or degree of spreading of the rays) is comparable to *C. intermedia*, but different from the uniform trichomes covering the upper surface of *Polianthion wichurae* or *Pol. minutiflorum* (Fig. 3C, L).

Epidermal sculpturing of the surface was observed in all species, except *Cryptandra intratropica*, due to the dense cover of trichomes on the upper surface. Parallel striate patterns are present on *C. lanosiflora* (Fig. 11A). The five remaining species have a characteristic punctate pattern on all cells of the epidermis (e.g. Figs 10D, 11D, G, J). This punctate surface is different to the one observed in *Pomaderris elliptica*, since in that species the centre of each epidermal cell seems to be slightly sunken (Fig. 8A; see above).

Two types of indumentum were found on the lower surface of *Cryptandra* species. The lower surface of *Cryptandra amara* and *C. mutila* is totally glabrous, with only a few appressed antrorse simple hairs along the midrib. The exception was one appressed stellate trichome with umbo present on the *C. mutila* specimen examined (Fig. 11L). This is the first report of stellate hairs on *C. mutila*, which so far was thought to be one of only a few species of Pomaderreae without stellate hairs (K.R. Thiele, pers. comm.).

The remaining taxa have a moderate to dense indumentum of stellate trichomes (fasciculate, appressed stellate and multiradiate hairs) on the lower surface. The leaf is usually closely revolute and obscuring the lower surface. In *Cryptandra dielsii* and *C. intermedia* the lower surface is totally obscured (Figs 10H, I, 11E, F), whereas in *C. lanosiflora* and *C. connata* the midrib is exposed and then covered with long antrorse simple hairs (Fig. 11B, C, H, I).

Cryptandra intratropica has more or less flat leaves with a dense stellate indumentum on the lower surface of the leaf (Fig. 10K, L). Morphologically, it is closely related to *C. filiformis* A.R.Bean and *C. triplex* K.R.Thiele ex Kellermann, two species of *Cryptandra* that share the dense stellate indumentum with *C. intratropica*, in addition to inflorescence and floral characteristics (Kellermann 2006).

Conclusion

The indumentum of the leaves of Pomaderreae was examined with Scanning Electron Microscopy for 32 species. Although this was only a limited sample set, preliminary conclusions can be drawn on the taxonomic significance and function of the trichomes.

A dense indumentum on the lower surface of the leaves was found in nearly all taxa. The main function of these hairs may be the prevention of water loss, which is particularly important in arid ecosystems (Ehleringer 1984). In many Pomaderreae species that occur in arid or semi-arid environments, this is paired with xerophytic, strongly recurved or revolute leaves, which fully or partly obscure the lower surface, e.g. in *Cryptandra dielsii* (Fig. 11F), *Siegfriedia darwinioides* (Fig. 10C) or *Spyridium furculentum* (Fig. 4K).

Species of *Stenanthemum* (Fig. 5H, F), *Serichonus gracilipes*, *Papistylus grandiflorum* and *Blackallia nudiflora* (Fig. 6B, E, H), *Trymalium wayi* (Fig. 7H) and *Polianthion collinum* (Fig. 3H), which grow in similar arid conditions, meet this environmental challenge with incurved conduplicate leaves (e.g. Fig. 6F) that are covered in a dense layer of long appressed simple hairs on the lower surface (the outer surface in conduplicate leaves). This silky or villous layer is usually white, grey or silver in colour, presumably reflects the sunlight, and therefore decreases the amount of radiation absorbed by the leaf (Holmes & Keiller 2002). This effect is reinforced by folded leaves, i.e. only very little sunlight is actually received by the upper (inner) surface of the leaves. A decrease in leaf temperature also helps to reduce transpiration (Johnson 1975).

Many species of *Pomaderris*, *Trymalium* and *Spyridium* occur in mesic environments, e.g. *T. odoratissimum* in the forests of south-west Western Australia. These species have larger leaves, which are covered in a variety of indumenta. Prevention of water loss during the summer months might be one explanation for the development of complex stalked and dendroid trichomes of *Pom. aspera* or *Pom. racemosa* (Fig. 9). However, an additional explanation for the development of these hairs could be defence against predators (Johnson 1975), which find it much easier to eat the large soft leaves of *Trymalium* or *Pomaderris*, compared to the xerophytic hard leaves of, for example, *Cryptandra* or *Siegfriedia*. The deposition of eggs may be obstructed by trichomes (Levin 1973). There is also evidence that leaf indumentum protects against parasitic algae, fungi and bacteria (Johnson 1975).

The indumentum on the upper surface of the leaves is more variable within genera and even within species (*cf.* Ross 1990 for *Pom. prunifolia*). Many species of *Spyridium* and *Stenanthemum* develop floral leaves around the inflorescences. These special leaves are covered in a conspicuous white, dense and felty indumentum and are thought to attract pollinators to the flowers. The minute flowers within one head-like inflorescence of *Spyridium* and *Stenanthemum* (containing up to 50 flowers in some species) usually bloom over a long period, with only one or two flowers being open at a time. Attracting possible pollinators with 2–6 floral leaves seems to be a better expenditure of resources for the plant, than producing large showy individual flowers. In a way, taxa with floral leaves mimic the appearance of capitula of Asteraceae.

A dense cover of stellate hairs on the upper surface of the leaves is also present in a number of unrelated taxa that occur in the tropical north of Australia, such as *Cryptandra filiformis* (Bean 2004), *C. intratropica* (Fig. 10J, L), *Pomaderris tropica* (Ross 1990) or *Polianthion minutiflorum* (Fig. 3J, L). It is possible that this is in response to higher exposure to sun and increases the reflectance of the leaves.

It is interesting to note that the only species in Pomaderreae that is totally glabrous, *Trymalium monospermum*, has a conspicuous glaucous, waxy epidermis (pers. obs.) and adapted to the arid environment by increasing surface wax production instead of a dense indumentum. It is not known, whether other species of Australian Rhamnaceae have waxy leaves.

Trichomes and indumenta on leaves of species of Pomaderreae are not always constant within genera or groups of species, but often variable, a fact that might reflect the development of indumenta being mostly associated with their function rather than with the phylogeny of species. However, in some groups, such as *Stenanthemum*, *Cryptandra* or the three small genera *Blackallia*, *Serichonus* and *Papistylus*, indumentum characters seem more constant and might be of value when defining genera and elucidating relationships between taxa. The examination of more species with SEM is needed to complete the data-set and to be able to draw firm conclusions on the taxonomic significance of leaf indumentum in the 'Australian stellate-haired Rhamnaceae'.

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Taxonomic evaluation of *Ptilotus manglesii* (Amaranthaceae) and recognition of *P. davisii* for two phrase names in south-west Western Australia

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Abstract: Evaluation of *Ptilotus manglesii* (Lindl.) F.Muell. (Amaranthaceae) and two phrase-named taxa from south-west Western Australia support recognition of the new species *Ptilotus davisii* T.Hammer. The new species is morphologically similar to *P. manglesii*, but clearly differentiated from it in vegetative and floral characters. The differences between *P. manglesii* and *P. davisii* are discussed and a key is provided. The taxonomic and nomenclatural history of *P. manglesii* is also discussed and lectotypifications are made.

Keywords: Amaranthaceae, new species, nomenclature, *Ptilotus*, taxonomy, typification

Introduction

Ptilotus R.Br. (Amaranthaceae) includes approximately 120 species, of which 93 are native to Western Australia (Hammer *et al.* 2018). Most species occur in arid and semi-arid regions of Australia, while smaller numbers are native to mesic climates (see Hammer 2019). *Ptilotus manglesii* (Lindl.) F.Muell., commonly "pom pom" or "rose-tipped mulla mulla", is endemic to the winter-wet Mediterranean climate of the Southwest Australian Floristic Region, a global biodiversity hotspot (Hopper & Gioia 2004).

Ptilotus manglesii was originally included within *Trichinium* R.Br. as *T. manglesii* Lindl. (Lindley 1839). *Trichinium* and *Ptilotus* were described by Brown (1810), who considered them to be close, but differentiated on the basis of *Trichinium* having more hairs on the exterior surface of the flowers. Poiret (1816) was not convinced that the genera were distinct and therefore chose to unite them as separate sections under the name *Ptilotus*. Despite this early synonymisation, many authors (e.g. Lindley 1839; Fielding & Gardner 1844; Moquin-Tandon 1849; Bentham 1870) continued to recognise *Trichinium* as distinct from *Ptilotus*, while other authors (e.g. Mueller 1868, 1882; Schinz 1893) continued to include *Trichinium* under *Ptilotus*. The genera have remained united since Black (1948). The union of the two genera is supported by recent molecular phylogenies (e.g. Hammer *et al.* 2019b), which indicate that they are not reciprocally monophyletic. See Hammer (2019) for further discussion on the taxonomic history of *Ptilotus* and *Trichinium*.

Fielding and Gardner (1844) included an illustration and description of *Trichinium manglesii* and erected *T. spectabile* Fielding & Gardner, which they differentiated from *T. manglesii* on the basis of its longer linear leaves (as opposed to broader and more spathulate leaves in *T. manglesii*). Moquin-Tandon (1849) included both species in his treatment of *Trichinium* and recognised the new variety *T. manglesii* var. *angustifolium* Moq., distinguishing it from var. *manglesii* on the basis that it had longer and narrower leaves. Although Moquin-Tandon included *T. spectabile* in his treatment, he was not convinced that it was distinct from *T. manglesii* var. *angustifolium*, adding the note "An [or] *T. manglesii* var. *angustifolium*?" under the description of *T. spectabile* (Moquin-Tandon 1849: 289).

Mueller (1868) combined all species of *Trichinium* under *Ptilotus*, and treated *T. spectabile* as a synonym of his new combination *P. manglesii*. Bentham (1870) did not follow Mueller in the synonymisation of the genera, but did, however, follow him in including *T. spectabile* under *T. manglesii*, remarking "the broad and narrow-leaved specimens, distinguished as *T. manglesii* and *T. spectabile*, are so much intermixed and connected by intermediates that they cannot be reckoned as marked varieties" (Bentham 1870: 228). No mention was made by either author of Moquin-Tandon's *T. manglesii* var. *angustifolium*. Since Mueller and Bentham's broader circumscriptions of *P. manglesii*, the taxonomy of this species has remained stable.

Several specimens were collected in the southern part of the range of *Ptilotus manglesii* from 1992 to 2005

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that were initially included within the morphological variation of *P. manglesii*, or as *P.* aff. *manglesii*. These specimens varied from the typical *P. manglesii* in being smaller plants with shorter inflorescences and flowers and having narrower basal leaves at the level of or extending above the inflorescences (i.e. having leaves longer than flowering stems). The growing number of specimens with this morphology led to the erection of two phrase-names at the Western Australian Herbarium (PERTH), *Ptilotus* sp. Beaufort River (*G.J. Keighery 16554*) in 2004 and *P.* sp. Porongurup (*R. Davis 10805*) in 2005. *Ptilotus* sp. Porongurup was differentiated from the earlier phrase-name due to its ovoid inflorescences (subsequent specimens were globose) and a slightly shorter and denser abaxial sepal indumentum (R. Davis, pers. comm.). The present study evaluates the status of these phrase-names with respect to the morphological variability of *P. manglesii* across its geographic range.

Methods

This study was based on examination of dried specimens of *Ptilotus manglesii*, *P.* sp. Beaufort River and *P.* sp. Porongurup housed at PERTH. Specimens were critically evaluated irrespective of current determinations and compared to the protologues and type specimens. Scans of type specimens were accessed through JSTOR Global Plants (https://plants.jstor.org/) and the herbarium catalogues of Kew (https://apps.kew.org/herbcat/gotoHomePage.do) and Museum National d'Histoire Naturelle (https://science.mnhn.fr/institution/mnhn/collection/p). The staff at the National Herbarium of Victoria (MEL) kindly arranged for type specimens to be scanned and made available for use in this study.

Results and discussion

No morphological characters were found that clearly segregate the specimens of *Ptilotus* sp. Beaufort River from those of *P.* sp. Porongurup. Measurements of floral and vegetative characters for the two phrase names overlap considerably. The differentiation of *P.* sp. Porongurup from *P.* sp. Beaufort River on the basis of having a slightly shorter and denser abaxial sepal indumentum was not supported with close examination of the specimens currently available. The density and length of the sepal indumentum was found to vary throughout the range of both phrase names, and no further characters were found with which to segregate them. *Ptilotus* sp. Beaufort River and *P.* sp. Porongurup are therefore recognised here as the same taxonomic entity. For convenience, the combined entity is referred to using the earlier name *P.* sp. Beaufort River in the remainder of this discussion.

The geographic range of *Ptilotus manglesii* overlaps entirely with that of the known distributions of *P.* sp. Beaufort River (Fig. 1). At several locations of *P.* sp. Beaufort River, plants occur in close proximity to, or co-occur with populations of *P. manglesii* (e.g. *R. Davis 12974* and *R. Davis 12975*; Fig. 2A, C). Examination of specimens in the field and herbarium indicates that *P. manglesii* is morphologically consistently separable from *P.* sp. Beaufort River, with no apparent intermediates, using several easily diagnosable characters.

Plants of *Ptilotus* sp. Beaufort River are conspicuously shorter than *P. manglesii*, have narrower leaves that are often longer than the flowering stems and inflorescences, and often have leaves and flowering stems densely clustered (Fig. 2). As noted by previous authors (e.g. Mueller 1868; Bentham 1870), *P. manglesii* is morphologically diverse in its vegetative characters, yet it never has flowering stems shorter than the long and narrow basal leaves. Leaves of *P. manglesii* range in shape from spathulate (as described in the protologue), to narrowly oblanceolate, as described for *T. spectabile* and *T. manglesii* var. *angustifolium*. Narrow-leaved specimens of *P. manglesii*, previously included within the concepts of *T. spectabile* and *T. manglesii* var. *angustifolium*, can be differentiated from *P.* sp. Beaufort River by being taller plants (to 30 cm high) with flowering stems that are consistently longer than the basal leaves.

In addition, *Ptilotus manglesii* and *P.* sp. Beaufort River can be reliably segregated by the sizes of several floral structures. Bracts, bracteoles and outer sepals in *P. manglesii* are 10–13.5 mm long, 13–15 mm long and 17–28 mm long, respectively, and are disjunctly longer than those of *P.* sp. Beaufort River (6.8–9 mm long, 6.2–11.5 mm long and 9–14.5 mm long, respectively). Sepal length is related to inflorescence width, which is also conspicuously different between *P. manglesii* and *P.* sp. Beaufort River, the former having longer and broader inflorescences (38–50 mm wide) than the latter (20–40 mm wide). Anthers in *P. manglesii* are longer than in *P.* sp. Beaufort River (1.0–1.2 mm long *vs.* 0.5–0.7 mm long), as are staminodes (2.5–5.0 mm *vs.* 1.1–2.3 mm long) and styles (4.0–6.5 mm long *vs.* 1.4–3.5 mm long).

Given the morphological segregation from *P. manglesii*, the new species *Ptilotus davisii* T.Hammer is formally erected here to accommodate the entity previously recognised under the phrase names *P.* sp. Beaufort River (*G.J. Keighery 16554*) and *P.* sp. Porongurup (*R. Davis 10805*).

Key to species

1. Bracts 10–13.5 mm long; bracteoles 13–15 mm long; outer sepals 17–28 mm long; anthers 1.0–1.2 mm long; style 4.0–6.5 mm long . . . . . *Ptilotus manglesii*

1: Bracts 6.8–9.0 mm long; bracteoles 6.2–11.5 mm long; outer sepals 9.0–14.5 mm long; anthers 0.5–0.7 mm long; style 1.4–3.5 mm long . . . . . *Ptilotus davisii*

Taxonomy

Ptilotus davisii T.Hammer, ***sp. nov.***

Holotypus: c. 2.1 km S along Knight Road from the junction with Washpool Road, Woogenellup, Western Australia, 10 Dec. 2018, *R. Davis & T. Hammer RD 12985* (PERTH09127933). **Isotypus:** CANB [to be distributed]. Fig. 2D, E.

Ptilotus sp. Beaufort River (*G.J. Keighery 16554*) Western Australian Herbarium, *FloraBase* https://florabase.dpaw.wa.gov.au/ [accessed: 1 Apr. 2020].

Ptilotus sp. Porongurup (*R. Davis 10805*) Western Australian Herbarium, *FloraBase* https://florabase.dpaw.wa.gov.au/ [accessed: 1 Apr. 2020].

Perennial *herbs* 40–150 mm high, 50–200 mm wide; tap root woody. *Stems* multiple, decumbent or erect, 10–60 mm long, terete, ribbed, glabrescent with shortly verticillate hairs. *Basal leaves* linear to oblanceolate, 40–150 mm long, 0.5–7 mm wide, glabrous or glabrescent with shortly verticillate hairs; base sessile, broadened into a persistent sheath 1–4 mm wide; margins entire; apex acute or rounded. *Cauline leaves* linear to narrowly lanceolate, 10–30 mm long, 0.5–4 mm wide, glabrous or with shortly verticillate hairs on the margins; base sessile, attenuate; margins entire; apex acute. *Inflorescences* terminal, spiciform, hemispherical to globular or rarely ovoid, 10–35 mm long, 20–40 mm wide, pink or magenta. *Bracts* ovate, 6.8–9.0 mm long, 2.5–3.5 mm wide, brown or white, with scattered verticillate hairs to 2 mm long; midrib not prominent; apex acute. *Bracteoles* ovate, 6.2–11.5 mm long, 2.6–3.9 mm wide, transparent, glabrous apart from midrib; midrib prominent, with verticillate hairs to 3 mm long; apex brown, acute. *Outer sepals* lanceolate with a dilated apex, ± straight, 9–14.5 mm long, 1.1–2.1 mm wide; inner surface glabrous; outer surface with verticillate hairs to 5 mm long and a distally glabrous portion to 3 mm long; apex dilated, truncate, serrate, with ± in-rolled margins. *Inner sepals* lanceolate with a dilated apex, ± straight, 8.2–14 mm long, 1.0–1.6 mm wide; inner surface glabrous apart from a fringe of straight verticillate hairs to 1 mm long on the margins half-way up the sepal length, and woolly hairs to 2 mm long at the base; outer surface with verticillate hairs to 1.5 mm long and a distally glabrous portion to 3 mm long; apex dilated, truncate, serrate, with ± in-rolled margins. *Fertile stamens* 3–5; *filaments* uneven in length, 2.0–5.6 mm long; *anthers* 0.5–0.7 mm long, 0.3–0.5 mm wide, pink. *Staminodes* 0–2, 1.1–2.3 mm long. *Staminal cup* 0.4–0.7 mm long, symmetrical, lacking appendages. *Ovary* obconical, 1.3–1.9 mm long, 0.9–1.5 mm wide, glabrous; *stipe* 1.5–2.5 mm long, tightly enclosed by sepal bases at maturity. *Style* curved, 1.4–3.5 mm long, excentric on the ovary apex. *Stigma* unlobed, capitate. *Seed* not seen. **Fig. 2C–E.**

Diagnostic features. *Ptilotus davisii* may be distinguished from all other members of the genus by the following combination of characters: a small perennial herb to 15 cm high, basal leaves 0.5–7 mm wide and usually longer than the stems, inner and outer sepals less than 15 mm long, outer sepal surface pink or magenta, inner surface of sepals with a basal woolly indumentum, anthers 0.4–0.7 mm long, style excentric on the ovary apex, a glabrous ovary, style curved and 1.4–3.5 mm long.

Phenology. Most flowering and fruiting specimens have been collected in late spring to summer (November to February).

Distribution and habitat. *Ptilotus davisii* occurs in the Avon Wheatbelt, Jarrah Forest and Esperance Plains IBRA (Interim Biogeographical Regionalisation for Australia) regions of south-west Western Australia, from 33.0° S to 34.6° S latitude and 116.4° E to

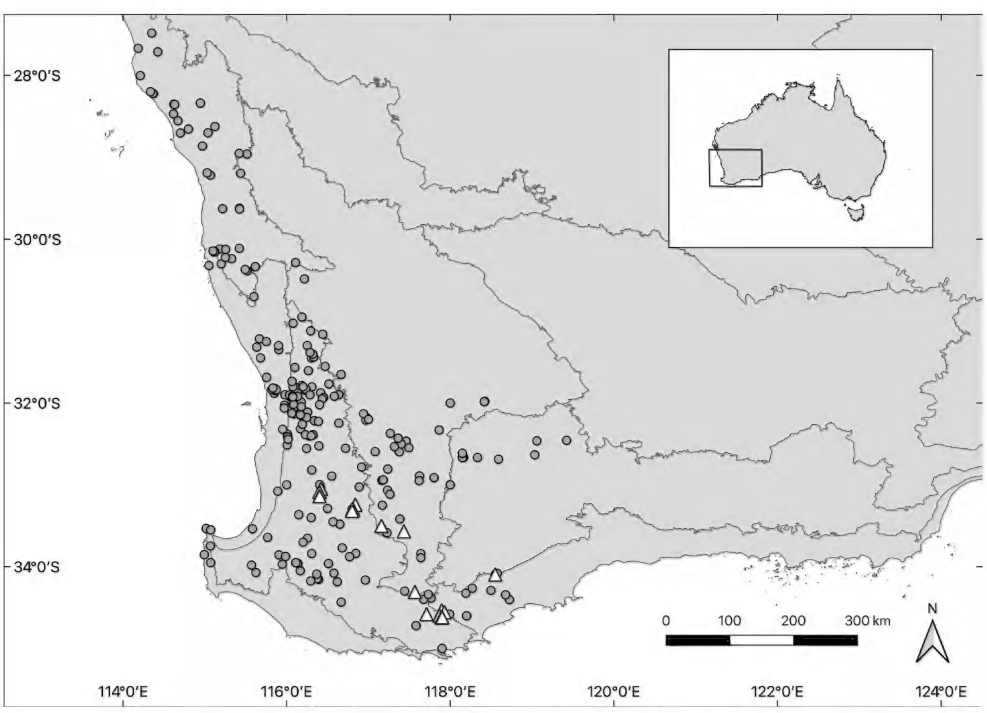

Fig. 1. Locations for the PERTH specimens of ***Ptilotus manglesii*** (grey circles) and ***P. davisii*** (white triangles). Boundaries are Interim Biogeographic Regionalisation for Australia (IBRA) regions (Department of the Environment 2018).

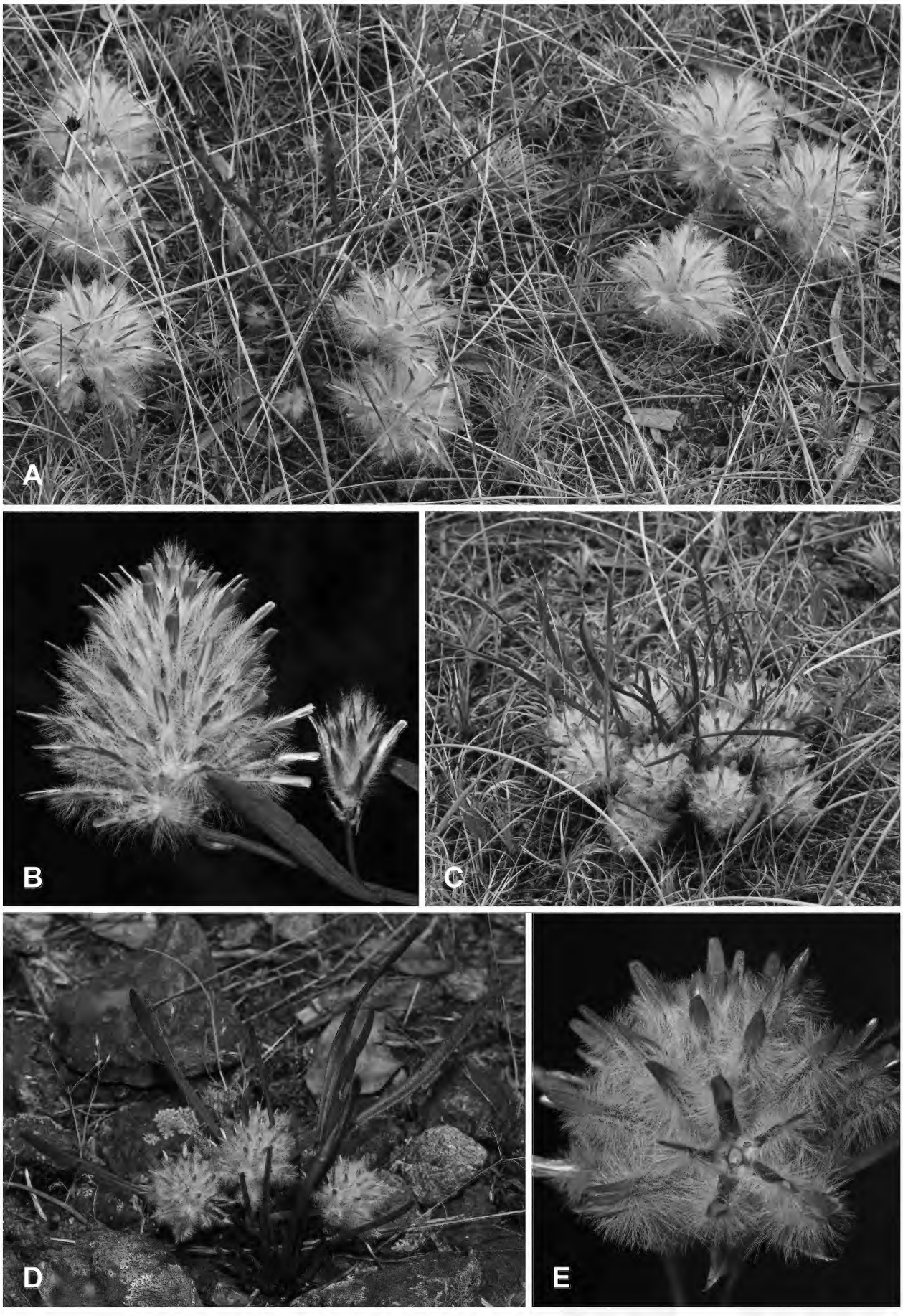

Fig. 2. ***Ptilotus manglesii***: **A** habit; **B** inflorescence. ***Ptilotus davisii***: **C**, **D** habit; **E** inflorescence. — A *R. Davis 12975*, B *T. Hammer & R. Davis TH 76*, C *R. Davis 12974*, D, E *R. Davis & T. Hammer RD 12985*. A and C were collected from the same location. Photos: A, C–E R. Davis; B T. Hammer.

118.5° E longitude (Fig. 1). It has been collected growing in seasonally wet plains, creek lines, and roadside drainage lines in grey or brown sandy loam or clay, occasionally with ironstone or laterite. It has been commonly collected in *Eucalyptus wandoo* woodlands and *Melaleuca* shrublands.

Conservation status. *Ptilotus davisii* is not currently listed as of conservation concern in Western Australia.

Proposed Vernacular Name. Davis's mulla mulla.

Etymology. The specific epithet honours the Western Australian botanist Robert W. Davis (1959–), who has made the majority of known collections of the species and was the first to recognise it as potentially being a new taxon (R. Davis, pers. comm.). Davis has made substantial contributions to the taxonomy of many Western Australian plant groups during his long career at the Western Australian Herbarium, including authoring 16 *Ptilotus* taxa and publishing several important taxonomic revisions in the genus.

Other specimens examined

WESTERN AUSTRALIA: Boundary Road, 13 km NW of Quindanning, 5 Aug. 1997, *G. Paull 943A* (PERTH); c. 8 km S along Boundary Road from junction of Harvey-Quindanning Road, 13 Nov. 2015, *R. Davis & A. Brown RD 12587* (PERTH); c. 11 km N along Boundary Road from junction of Williams-Collie Road, c. 33 km NE of Collie, 13 Nov. 2015, *R. Davis & A. Brown RD 12586* (PERTH); 750 m S along Dardadine-Hillman Road from junction with Dardadine West Road, 11 Dec. 2018, *R. Davis & T. Hammer RD 12988* (PERTH); Hillman Townsite, 24 Nov. 1992, *V. Crowley DKN 166* (PERTH); c. 300 m N along Dardadine-Hillman Road from the junction with Howie Road, 1 Dec. 2018, *R. Davis 12974* (PERTH); 3.6 km N along Hillman Road from junction with Coalfields Highway, 11 Dec. 2018, *R. Davis & T. Hammer RD 12986* (PERTH); Hillman Townsite Reserve, Darkan, 14 Dec. 2000, *V. Crowley s.n.* (PERTH06005837); Beaufort River Water Reserve, Arthur River to Kojonup, *G.J. Keighery 16554* (PERTH); 3 km due E on Woodanilling-Robinson Road, Woodanilling, 6 Dec. 2008, *R. Garstone s.n.* (PERTH08472505); 21 km S of Ongerup on Boxwood-Ongerup Road, 20 Jan. 2006, *S. Osborne 125* (PERTH); Cranbrook catchment, 2 km E of Cranbrook, 10 Dec. 1996, *R. Davis 1727* (PERTH); 3.7 km W along Woogenellup Road from junction of Kalgan Plains Road, c. 7.5 km NNW of Kamballup, 31 Dec. 2005, *R. Davis 10961* (PERTH); 0.9 km S along Kalgan Plains Road from Woogenellup, 28 Dec. 2005, *R. Davis 10958* (PERTH); c. 75 m E along Woogenellup Road from the junction with Great Southern Railway Road, 10 Dec. 2018, *R. Davis & T. Hammer RD 12984* (PERTH); Twin Creek Conservation Reserve, Knight Rd, N of Porongurups, 18 Nov. 2005, *E.M. Sandiford 1129* (PERTH); Twin Creeks Nature Reserve, 4 km N of Porongurup, 28 Dec. 2005, *R. Davis 10959* (PERTH); 4 km N of Porongurup, Twin Creeks Reserve, Feb. 2005, *A. Burchell s.n.* (PERTH07395019); 4 km N of Porongurup, Twin Creeks Reserve, Jan. 2005, *A. Burchell s.n.* (PERTH07395027); Twins Creek Reserve, off Knights Road, c. 4 km N of Porongurup, 22 Dec. 2004, *R. Davis 10805* (PERTH).

Ptilotus manglesii (Lindl.) F.Muell.

Fragm. 6: 230 (1868). — *Trichinium manglesii* Lindl., *Edwards's Bot. Reg.* 25: sub tab. 28 (1839). — **Type citation:** "Swan River". **Syntype:** Western Australia, *Toward 46* (CGE?, *n.v.*), *fide* Benl (unpubl.).

Trichinium spectabile Fielding & Gardner, *Sert. Pl.* tab. 53 (1844). — **Type citation:** "Swan River Colony, New Holland. *Drummond n.* 436". **Lectotype (here designated):** Western Australia, 1839, *J. Drummond 436* (K000356849, ex Herb. Hooker; photo seen). **Isolectotypes:** K000356856, MEL2221664, MEL221665, MEL2217630, P04944200, P04944201, P04944250 (photos seen); PERTH 00336645!

Trichinium manglesii var. *angustifolium* Moq. in A.DC., *Prodromus* 13(2): 289 (1849). — **Type citation:** "Drummond! Preiss! n. 1358.". **Lectotype (here designated):** "Nova Hollandia, Swan River", 1839, *J. Drummond s.n.* (P00609983, ex Herb. Moquin-Tandon; photo seen). **Isolectotype:** K000356855 (photo seen). **Remaining syntypes:** Port Leschenault, [Western Australia,] 28 Dec. 1839, *L. Preiss 1358* (L1695387, LD1213215, MEL2217614, MEL2217615, MEL2217617, P04944193, P04944197; photos seen)

Trichinium macrocephalum auct. non R.Br.: Nees in Lehm., *Pl. Preiss.* 1: 627 (1845).

Perennial *herbs* 100–400 mm high, 150–400 mm wide; tap root woody. *Stems* single or multiple, decumbent, prostrate or rarely erect, 70–300 mm long, terete, ribbed, glabrescent with shortly verticillate hairs. *Basal leaves* spathulate to oblanceolate, 40–150 mm long, 10–60 mm wide, glabrous or glabrescent with shortly verticillate hairs; base sessile, broadened into a persistent sheath 1–4 mm wide; margins entire or often undulating; apex acute or rounded. *Cauline leaves* lanceolate to ovate, 15–70 mm long, 5–15 mm wide, glabrous or with shortly verticillate hairs on the margins; base sessile, attenuate; margins entire or usually undulating; apex acute. *Inflorescences* terminal, spiciform, ovoid to cylindrical, 25–70 mm long, 38–50 mm wide, pink or magenta. *Bracts* ovate to lanceolate, 10–13.5 mm long, 2.8–4.5 mm wide, brown, with scattered verticillate hairs to 2.5 mm long in the basal half; midrib not prominent; apex acute. *Bracteoles* ovate to lanceolate, 13–15 mm long, 4.5–5.5 mm wide, transparent, glabrous apart from midrib; midrib prominent, with verticillate hairs to 3 mm long; apex brown, acute. *Outer sepals* lanceolate with a dilated apex, ± down-curved, 17–28 mm long, 2.0–4.0 mm wide; inner surface glabrous; outer surface with verticillate hairs to 5 mm long and a distally glabrous portion to 7 mm long; apex dilated, truncate, serrate, margins ± in-rolled. *Inner sepals* lanceolate with a dilated apex, ± down-curved, 15–25 mm long, 1.5–3.5 mm wide; inner surface glabrous apart from a fringe of straight verticillate hairs to 1 mm long on the margins half-way up the sepal and woolly hairs to 3 mm long at the base; outer surface with verticillate hairs to 4 mm long and a distally glabrous portion to 5 mm long; apex dilated, truncate, serrate, margins ± in-rolled. *Fertile stamens* 3–5; *filaments* unequal in length, 3.5–6.5 mm long; *anthers* 1.0–1.2 mm long,

0.5–0.6 mm wide, pink. *Staminodes* 0–2, 2.5–5.0 mm long. *Staminal cup* 0.5–1.0 mm long, symmetrical, lacking appendages. *Ovary* obconical, 2.0–2.7 mm long, 1.2–1.7 mm wide, glabrous; stipe 2.0–4.5 mm long, tightly enclosed by sepal bases at maturity. *Style* curved, 4.0–6.5 mm long, excentric on the ovary apex. *Stigma* unlobed, capitate. *Seed* dull brown, c. 3.1 mm long, c. 1.7 mm wide. **Fig. 2A, B.**

Phenology. *Ptilotus manglesii* is typically collected in flower and fruit from September to January, with populations in the north of the range flowering and fruiting earlier than in the south.

Distribution and habitat. *Ptilotus manglesii* occurs in south-west Western Australia from Kalbarri to Albany (i.e. 27.5° S to 35.0° S), and as far east as Hyden (i.e. 119.4° E) (Fig. 1). It can be found in a variety of habitats throughout its range, including open woodlands dominated by jarrah, marri or wandoo and open shrublands (e.g. with *Acacia* spp., *Allocasuarina* spp. or *Banksia* spp.) on slopes, road verges, drainage lines and seasonally wet plains. It grows in a variety of substrates, including red-, brown- or grey-coloured clay, loam or sand, often with gravel or laterite.

Conservation status. *Ptilotus manglesii* is not listed as of conservation concern.

Typification. Fielding & Gardner (1844) cited *Drummond 436* in the protologue of *Trichinium spectabile*. Of the available syntypes, the sheet K000356849 is here designated as the lectotype. The exsiccatum consist of seven inflorescences attached to stems with narrow basal and cauline leaves, which match the description and illustration in the protologue. The sheet is labelled "436. Swan River. Drummond" and "*T. spectabile* Field. Sert. t. 53" and bears the stamp "Herbarium Hookerianum 1867".

Further annotations were made on the sheet K000356849 by Bentham and Moquin-Tandon, indicating that they viewed this specimen in their treatments of *Trichinium* (see Moquin-Tandon 1849; Bentham 1870). Moquin-Tandon wrote on this specimen "*Trichinium manglesii* Lindl. var. *angustifolium* (an *T. speciosum* [sic] Field?)" and signed it "A. Moq", identifying the specimen as either *T. manglesii* var. *angustifolium* or *T. spectabile*. Perhaps because of this identification by Moquin-Tandon, the sheet was erroneously labelled "Type *Trichinium manglesii* var. *angustifolium*" at a later date by someone at K. Moquin-Tandon (1849) made it very clear in his treatment that he included this specimen under the concept of *T. spectabile*, as a narrow-leaved specimen of *Drummond 436*. He specified the material *J. Drummond s.n.* and *L. Preiss 1358* in the protologue of *T. manglesii* var. *angustifolium*.

Of the syntypes of *Trichinium manglesii* var. *angustifolium*, the specimen P00609983 of the gathering *J.Drummond s.n.* is here designated as the lectotype. The exsiccatum consists of a plant with a flowering inflorescence and long, narrow basal leaves attached to a rootstock, which matches the protologue in Moquin-Tandon (1849). The specimen was labelled by Moquin-Tandon as "*Trichinium manglesii* var. ß *angustifolium*" and is therefore considered likely to have been used by him for the description of this taxon.

Nomenclatural Notes. Lindley (1839) did not specify a collector in the protologue of *Trichinium manglesii*. Benl (unpubl.), in a manuscript for his treatment of *Ptilotus* for the Flora of Australia, indicated "*Toward 46* (CGE)" as the holotype. Andrew Toward was gardener to HRH the Duchess of Gloucester and was mentioned by Lindley (1839), along with Mangles, as sending him wild specimens of *Trichinium*. *Toward 46* (CGE) should be considered a syntype unless it can be established that it was the only specimen available to Lindley prior to finishing the protologue (ICN Art. 9.4; Turland *et al.* 2018; see also McNeill 2014). For the preparation of the present study, I have been unable to arrange to view this specimen or confirm its existence at CGE and cannot therefore resolve the status of the type for *T. manglesii*.

Other authors (e.g. Fielding & Gardner 1844; Mueller 1868; Bentham 1870) associated Lindley's concept with the gathering *Drummond 435*, presumably unaware of *Toward 46*. In November 1839, Drummond sent his first numbered collection of 1,300 specimens to Hooker in London (Erickson 1969), and among these were *Drummond 435* and *436*. Lindley completed the description of *Trichinium manglesii* in May 1839 (Lindley 1839), hence cannot have seen any numbered Drummond material (earlier collections of Drummond were un-numbered; Erickson 1969). Lindley may have seen earlier unnumbered specimens sent by Drummond. If the original material is not recovered, then a neotype should be designated for *T. manglesii* (ICN Art. 9.8 & 9.13; Turland *et al.* 2018).

Nees (1845) misapplied the name *Trichinium macrocephalum* R.Br. to the narrow-leaved specimen *L. Preiss 1358*, collected from Port Lechenault in Western Australia, which was later included as original material for *T. manglesii* var. *angustifolium* (Moquin-Tandon 1849). *Ptilotus macrocephalus* (R.Br.) Poir. (= *T. macrocephalum*) only occurs in south-eastern Australia and is not closely related to *P. manglesii* (see Hammer *et al.* 2019a, 2019b).

Selected specimens examined

WESTERN AUSTRALIA: 3 km NNE of Kalbarri, 24 Oct. 2000, *B.J. Lepschi et al. 4334* (PERTH); Over the fence line at the western end of Yuna golf course, 30 Oct. 2003, *K.A. Shepherd & R.Bennett KS 915* (PERTH); 1.3 km S along first north from junction of Skipper, c. 25 km NE of Eneabba, 9 Nov. 2004, *R. Davis 10781* (PERTH); Hi Vallee property (D. & J. Williams) Warradarge, close to creekline near E boundary of property, 7 Dec. 2002, *M. Hislop 2907* (PERTH); 200 m N along Canning Road from junction of Masonmill Road, Carmel, 20 Nov. 2002, *R. Davis 10536*

(PERTH); 19.5 km E along Bindoon-Dewars Pool Road from Great Northern Highway, 9 Nov. 2015, *T. Hammer, R. Davis & K. Thiele TH 78* (PERTH); Site 11, Gorrie Road, 5.5 km SSE of Chidlow, 1 Nov. 1996, *R. Davis 1522* (PERTH); 425 m SW along a trail heading towards Bixton Street from Bickley Road, Kenwick, 25 Oct. 2015, *T. Hammer & R. Davis TH 76* (PERTH); Wadderin Reserve, c. 300 m E of Reservoir, N of Narembeen, 26 Sep. 2003, *M. Hislop & M. Griffiths WW 104.30* (PERTH); 1.3 km S along Kinsella Road from junction of Brookton Highway, 22 Jan. 2017, *T. Hammer & R. Davis TH 99* (PERTH); Site 32, E of Great Southern Highway, c. 8 km SSE of Beverley, 25 Oct. 2000, *R. Davis WW 32-13* (PERTH); North Dandalup Dam, off Hines Rd, on W boundary of State Forest, 15 Nov. 1996, *A. Markey 880* (PERTH); c. 300 m N along Dardadine-Hillman Road from the junction with Howie Road, 1 Dec. 2018, *R. Davis 12975* (PERTH); 4.1 km from Wrights Bridge towards Nannup on Balingup-Nannup Road, 6 Jan. 2000, *T.R. Lally & N.G. Lally TRL 1643* (PERTH); Seaton Ross Road c. 20 km NE of Manjimup, 29 Oct. 1998, *R. Davis 8414* (PERTH); Gravel Pit, Yerriminup Road, E off Albany Highway, 9 Dec. 1985, *E.J. Croxford 4355* (PERTH); 0.5 km along firebreak running SW of Bluff Knoll Road, 0.3 km from Chester Pass Road in Stirling Range National Park, 24 Oct. 2001, *E. Hickman & S. Gilfillan EJH 1751* (PERTH); Pallinup River, 18 km NW of Mount Groper, 15 Jan. 1985, *K.R. Newbey 10912* (PERTH); 0.3 km W along Woogenilup Road from junction of Chester Pass Road, 31 Dec. 2005, *R. Davis 10963* (PERTH); Hay River, 25 Nov. 1994, *G. Janicke JAN 009* (PERTH).

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SHORT COMMUNICATION

Validation of two fungal names in *Marasmius* Fr. (Marasmiaceae)

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When publishing *Marasmius vagus* F.E.Guard, M.D.Barrett & Farid (Crous *et al.* 2020) and *Marasmius lebeliae* F.E.Guard (Crous *et al.* 2019), the authors omitted the appropriate herbarium code when designating the types, which were lodged in the Queensland Herbarium (BRI). They only cited the type specimen accession numbers as "AQ1008080" and "AQ799986", respectively. Although the acronym AQ means 'Accession Queensland', and all collections with an AQ number are curated at the Queensland Herbarium, no direct reference was made in either publication to BRI. The names are therefore invalid as per Art. 40.7 of the *International Code of Nomenclature* (Turnland *et al.* 2018). We here validate both names, by presenting the corrected type citations along with references to the original descriptions. As required under Art F.5.7 (May *et al.* 2019), new identifiers for the names have been obtained from MycoBank.

Marasmius vagus* F.E.Guard, M.D.Barrett & Farid, *sp. nov.

Mycobank number: MB837473.

Marasmius vagus F.E.Guard, M.D.Barrett & Farid, *Persoonia* 44: 415 (2020), *nom. inval.* [Mycobank number: MB833552]; see here for validating description.

Holotypus: Australia, Queensland, Mt Carbine, S16°34'44.1" E145°11'13.7", in savanna grassland leaf litter, 7 Mar. 2018, *F. Guard & S. McMullanFisher SMF3041* (BRI AQ1008080; ITS and LSU sequences: GenBank MT117839 and MT110674)

Marasmius lebeliae* F.E.Guard, *sp. nov.

Mycobank number: MB837474.

Marasmius lebeliae F.E.Guard, *Persoonia* 42: 427 (2019), *nom. inval.* [Mycobank number: MB828485]; see here for validating description.

Holotypus: Australia, Queensland, Dilkusha Nature Refuge, Maleny, Site 1, in leaf litter and *Casuarina* needles under *Elaeocarpus grandis* and *Allocasuarina cunninghamiana*, in regenerating subtropical rainforest, 3 Feb. 2018, *F. Guard F2018011* (BRI AQ799986; ITS sequence GenBank: MK211200).

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Typification and identity of *Riccia macrospora* Stephani (Ricciaceae)

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Abstract: The typification, circumscription and distribution of the Australian endemic *Riccia macrospora* is clarified. Recognition of *Riccia macrospora* as a distinct species is supported, and similarities with the southern Australian *R. inflexa* are noted. Original material of *Riccia macrospora* is shown to be a mixed gathering, lectotypified by a specimen at G.

Keywords: *Riccia inflexa*, *Riccia limbata*, *Riccia rubrispora*, *Riccia runssorensis*, *Riccia sellingii*, liverworts, Australia

Introduction

While revising the genus *Riccia* L. for the monsoonal tropics of the Northern Territory, Australia, it became evident that the taxonomic status of some of the *Riccia* species occurring elsewhere in the Northern Territory, and potentially occurring in this northern region, required taxonomic attention. One of these species is the poorly known central Australian endemic *Riccia macrospora* Steph.

Materials and Methods

Type material of *Riccia macrospora* at AD, BM, G and MEL was examined (herbarium codes follow Thiers 2019). If plants were fertile, spores were carefully removed and mounted in water on microscope slides for light microscopy (LM) or mounted on double-sided sticky tape on aluminium stubs, sputter coated with platinum using a BAL-TEC SCD 005 Sputter Coater and viewed with a Phillips Scanning Electron Microscope (SEM).

Results and Discussion

Riccia macrospora was originally described by Franz Stephani in 1898 from a central Australian collection made by Richard Helms, naturalist on the Elder Exploring Expedition from May 1891–June 1892[1] (Helms collected the specimen together with several other liverworts at Arcoeillina Well[2], near the Everard Ranges, in north-western South Australia on 27 May 1891).

A portion of the collection was sent to Stephani for identification and he subsequently recognised it as a new species (Stephani 1898). Apart from his written description, Stephani also made several drawings of the gametophyte and a spore (Fig. 1) for his unpublished *Icones hepaticarum* (Stephani 1985). Specimens from Helms' collection, comprising original material of the name *Riccia macrospora* are held at AD, BM, G (where Stephani's herbarium is housed; see Stafleu & Cowan 1985) and MEL. Examination of this material by the authors indicates that Helms' gathering represents a mixed collection, as discussed below.

Na-Thalang (1980) included *Riccia macrospora* in her landmark revision of the genus *Riccia* in Australia and cited the type of the name as "Holotype: Central Australia. Arco-ellina [Arcoeillina] Well, *R.Helms*, 27.v.1891 (G 12730); isotype (AD 19)." This is here treated as effective lectotypification by Na-Thalang in accordance with ICN Art. 7.11 (Turland *et al.* 2018), and because Na-Thalang's citation meets the relevant requirements of Art. 7.11, her use of the term 'holotype' is correctable under Art. 9.10. Distinctive characters in Stephani's description that agree with the lectotype specimen held at G are the scales: "Squamae magnae, imbricatae, integerrimae, nigro-purpureae, frondis marginem longe superantes"[3] and the spores: "Sporae maximae 150μ, crebre, et regulariter lamellatae; anguli

1 https://www.anbg.gov.au/biography/helms-richard.html [accessed 21 Dec. 2018].

2 A photograph of the area can be found on the State Library of South Australia's image database, https://collections.slsa.sa.gov.au/resource/B+499/9 [accessed 29 Sep. 2020].

3 Translation: Scales large, imbricate, entire black-purple, from the margin of the frond long surpassing.

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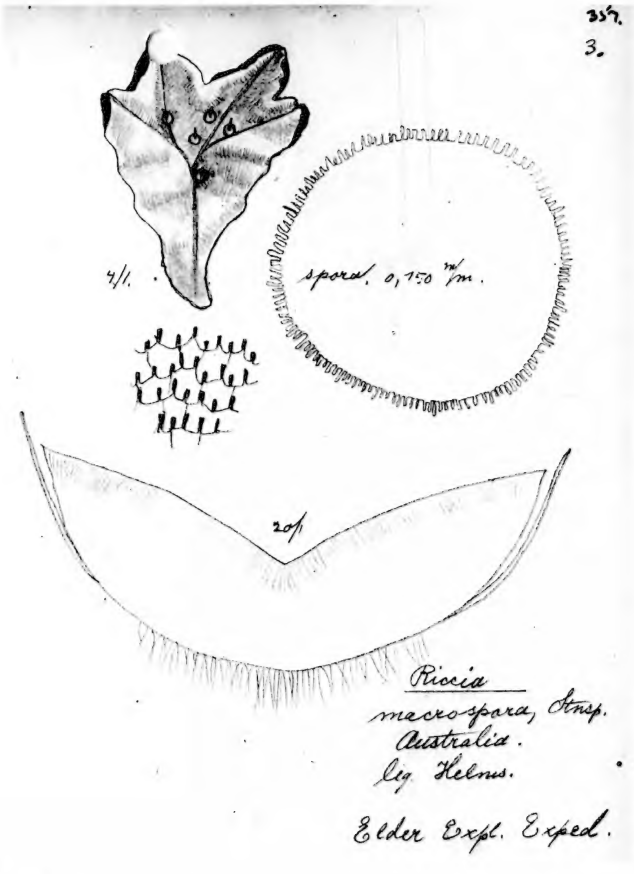

Fig. 1. Drawings of *Riccia macrospora* made by Franz Stephani for *Icones hepaticarum* (Stephani 1985).

lamellarum papilla alta truncate instructi, exosporium dein maxime hirtum."[4] When dry, the scales of the plants in the Geneva material are dark and almost black and extend beyond the margin of the thallus (observations by Beckmann of the actual specimen, and observations of lectotype image, Fig. 2A–B, and of two plant fragments seen by Cargill, sent by G for SEM spore observations). While spores sampled from this collection are less than 150 µm in diameter (up to 120 µm), as described by Stephani, they are still relatively large even when compared to other *Riccia* species. Stephani describes the patterning on the spores as "closely and regularly areolate, the corners of the areolae with high blunt papillae, exosporium elsewhere very hirsute". SEM images (Fig. 2C–F) of spores removed from the lectotype partially agree with the description in Stephani (1898), but do not necessarily match the subsequent illustration in Stephani's *Icones* which gives the impression of a spore that is quite 'hairy' around its circumference; that is, the spore bears numerous projections over its surface which appear as multiple spines around the circumference.

Material at BM (Figs 3–5) is identical to the lectotype at G and is regarded as an isolectotype. SEM photos of spores accompanying the BM specimen (Figs 4B–E, 5A–D, F) and re-examination of spores through light microscopy shows a pattern (Figs 4D–E, 5E) identical to that of the lectotype. Both have a more or less reticulate pattern with alveoli surrounded by tall vermiculate lamellae on the distal face. On the proximal face, is a pattern of low vermiculae-like lamellae surrounding more regular shaped holes. The spores are also surrounded by a distinct wing and bear three pores. The G and BM spores match closely the description given by Stephani of spores that are regularly reticulate, with truncated protuberances at the corners of the areolae (Stephani 1898).

The specimens held at AD and MEL (Figs 6, 7, 8) are both sterile and are relatively large when compared to the material at BM and G (Fig. 3B). Ventral scales in the AD and MEL material are maroon when dry and bright crimson when rehydrated (Figs 6, 8, 10), while those of the BM (Fig. 9) and G material are purplish-black when dry but vary from crimson to purplish-violet when rehydrated. Scales on specimens at AD and MEL (Fig. 10) are also larger and extend well beyond the margin of the thallus, curling over onto the dorsal edge while those of the plants from the BM and G specimens remain appressed to the ventral flank of the segments only extending slightly above it. For the most part the scales of the AD and MEL specimens are attached only at their base, unlike the scales of the plants from the G and BM specimens, which are closely appressed to the ventral flank. This morphology does not match any known Australian species and the AD and MEL material may represent a new taxon. The specimens at AD and MEL are accordingly regarded as excluded syntypes.

Previous researchers (e.g. Seppelt 1974, 1998; Na-Thalang 1980), have treated *Riccia macrospora* as a distinct taxon, and this view is supported here. Na-Thalang placed *R. macrospora* and three other species in her 'Group *Squamatae*, Subgroup *Macrospora*'. Group *Squamatae*, with the largest number of species, was defined by ventral scales "reaching to or extending beyond the margins" (Na-Thalang 1980). Subgroup *Macrospora* was defined by variable purple scales and globose spores with a similar reticulate pattern all over. Na-Thalang's description of scales as 'variable' refers to her experiments on plants identified as *R. macrospora* and the South African taxon *R. limbata* Bisch., misapplied by Na-Thalang to Australian material of *R. inflexa* Taylor. She found that under variable light and moisture conditions the scales of *R. macrospora* changed from purple to hyaline, while those of *R. limbata* stayed more or less constant (Na-Thalang 1969).

Na-Thalang's concept of *Riccia macrospora* was principally based on spore characters which she deemed to be more reliable than scale characters. Her concept of *R. macrospora* describes the spores as dark red-purple, globose, lacking a wing, regularly

4 Translation: Spores large, 150 µm, closely and regularly areolate, the corners of the areolae with high blunt papillae, exosporium elsewhere very hirsute.

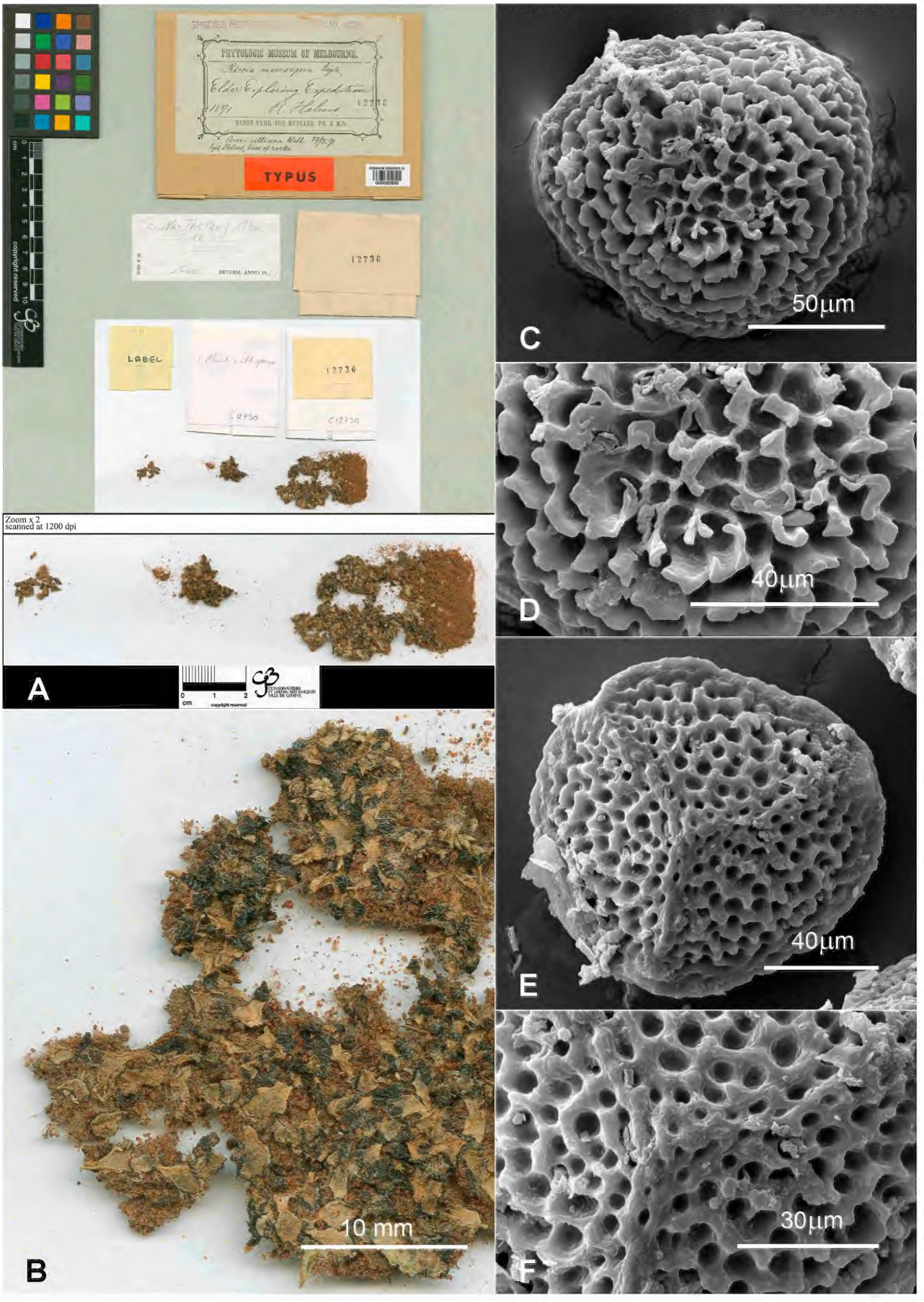

Fig. 2. *Riccia macrospora* lectotype (G00052600). **A** Whole specimen. **B** Close up view of dried plants. SEM images of spores. **C** Distal view of spore. **D** Magnified view of the patterning on the distal face. **E** Proximal view of spore. **F** Magnified view of patterning on the proximal face. — Image of herbarium specimen courtesy of Conservatoire et Jardin botaniques de la Ville de Genève, copyright owners.

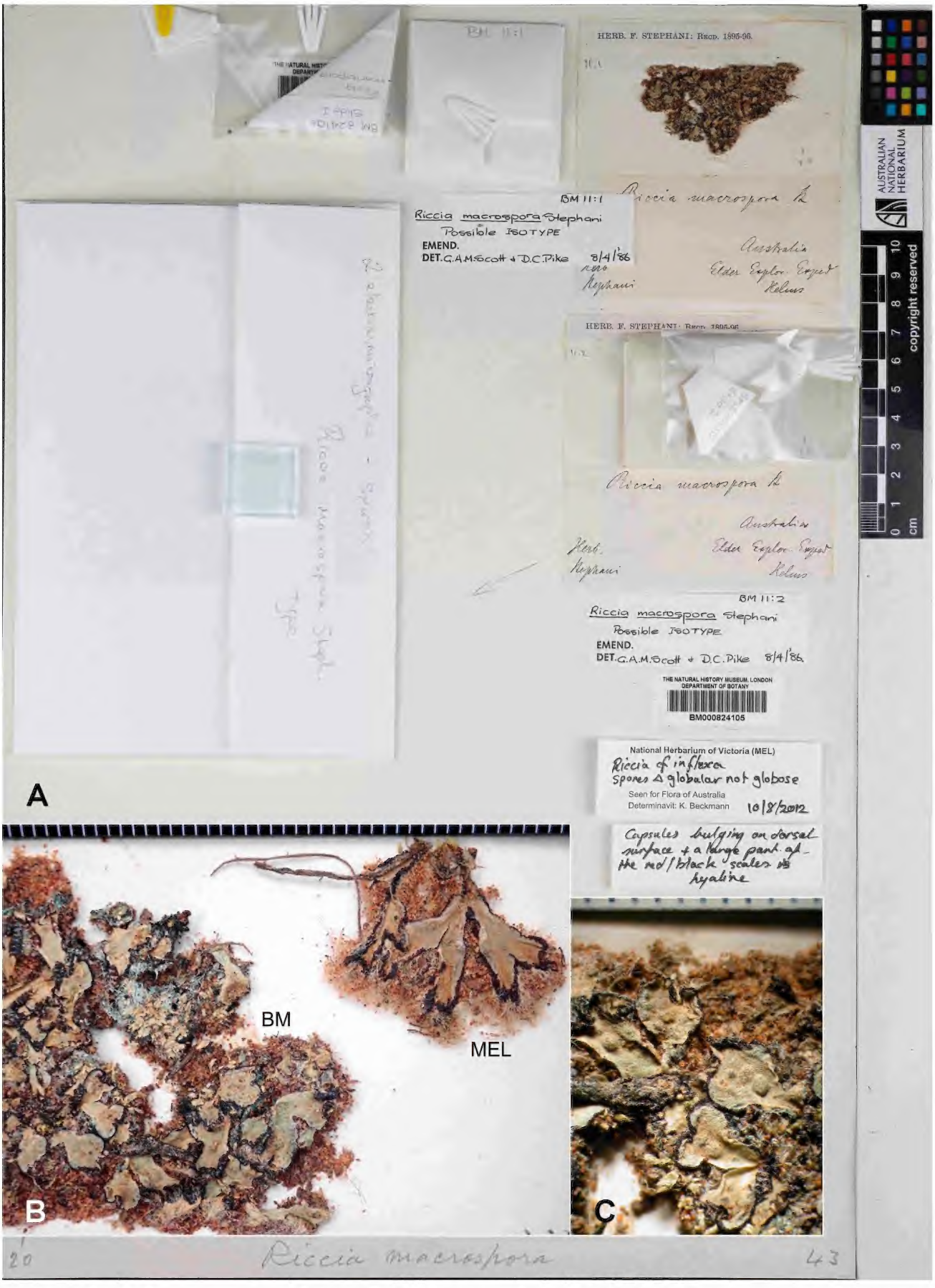

Fig. 3. *Riccia macrospora* isolectotype (BM). **A** Whole sheet. **B** Close up of dried plants with MEL specimen plants placed beside it for comparison. **C** Close up of plants (scale divisions = 1 mm). — BM000824105 & BM000824106 from the collections of the Natural History Museum, London, with permission to use images of specimen; photos taken by D.C. Cargill.

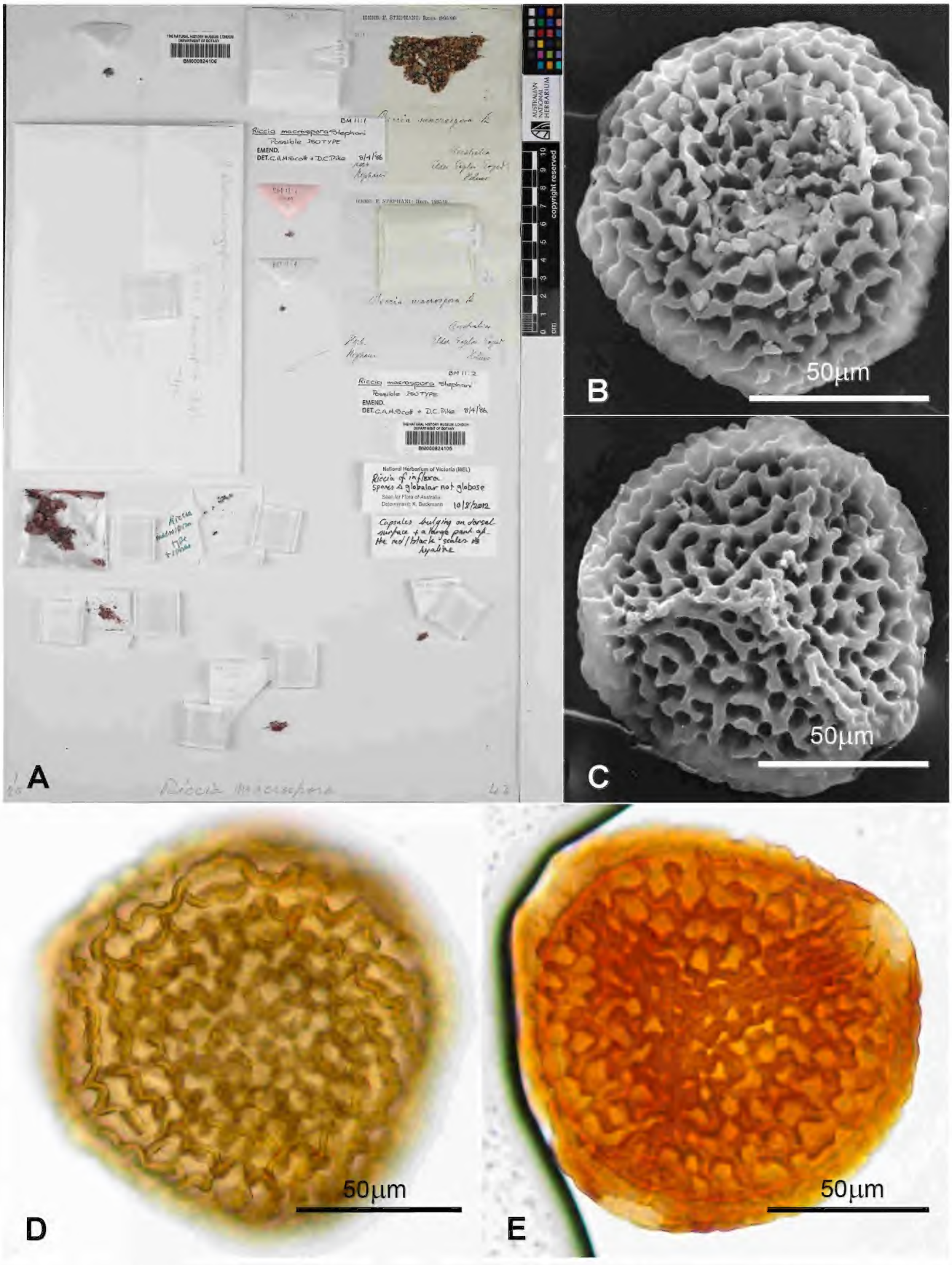

Fig. 4. *Riccia macrospora* isolectotype (BM). **A** Sheet with contents of all packets visible. **B** SEM image of distal view of spore. **C** SEM image of proximal view of spore. **D** Light micrograph of distal view of spore. **E** LM of proximal view of spore. — BM000824105 & BM000824106 from the collections of the Natural History Museum, London with permission to use images of specimen; photos taken by D.C. Cargill.

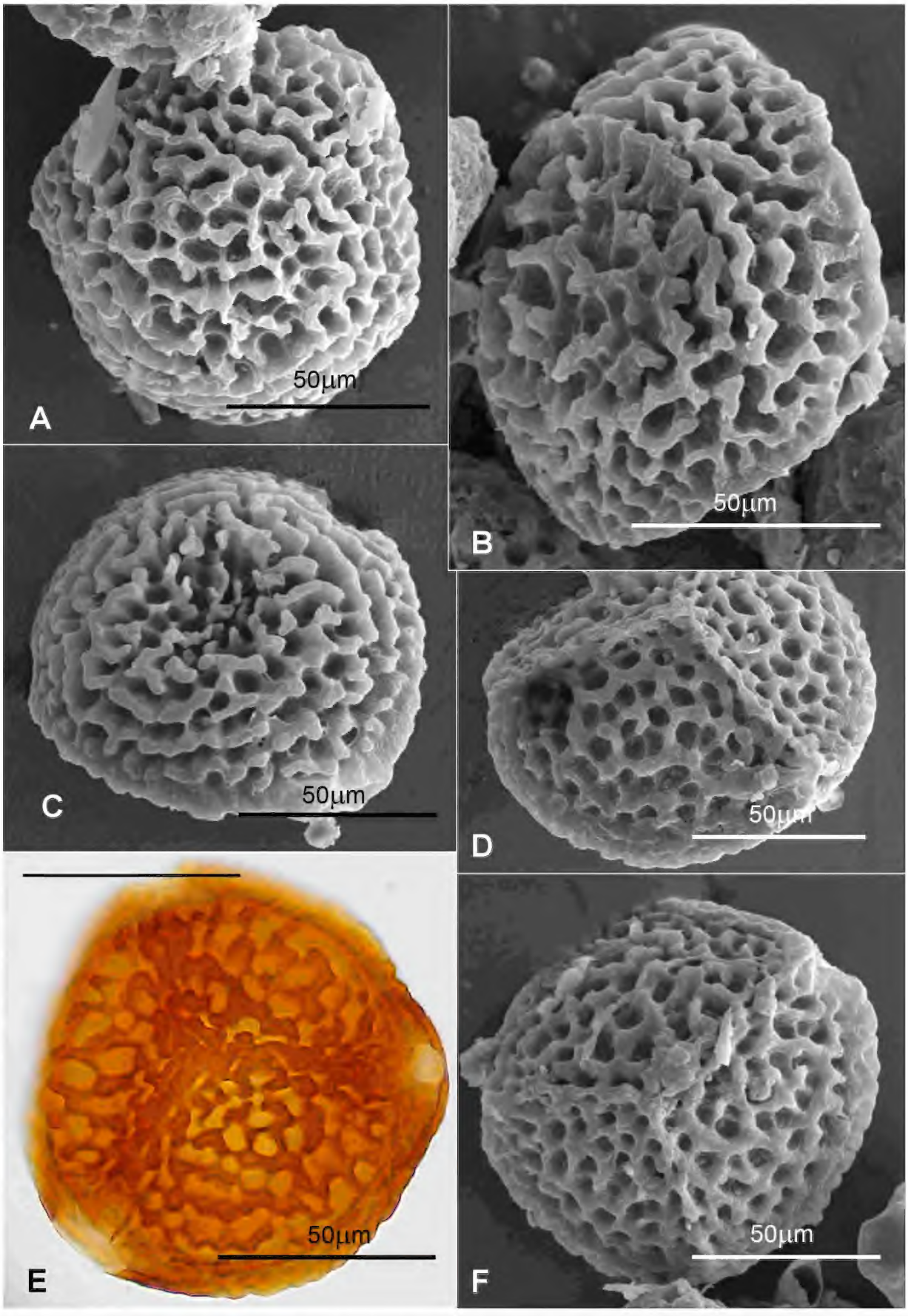

Fig. 5. *Riccia macrospora* isolectotype (BM). SEM and LM images of spores showing variation in the patterning for this species. **A** Distal view. **B** Lateral view of distal face. **C** Distal view. **D** Detail of one of the facets of the proximal face. **E** Proximal view showing the wing around the circumference of the spore and the three pores at the end of the triradiate arms. **F** Proximal view of spore. — BM000824105 & BM000824106 from the collections of the Natural History Museum, London with permission to use images of specimen; photos taken by D.C. Cargill.

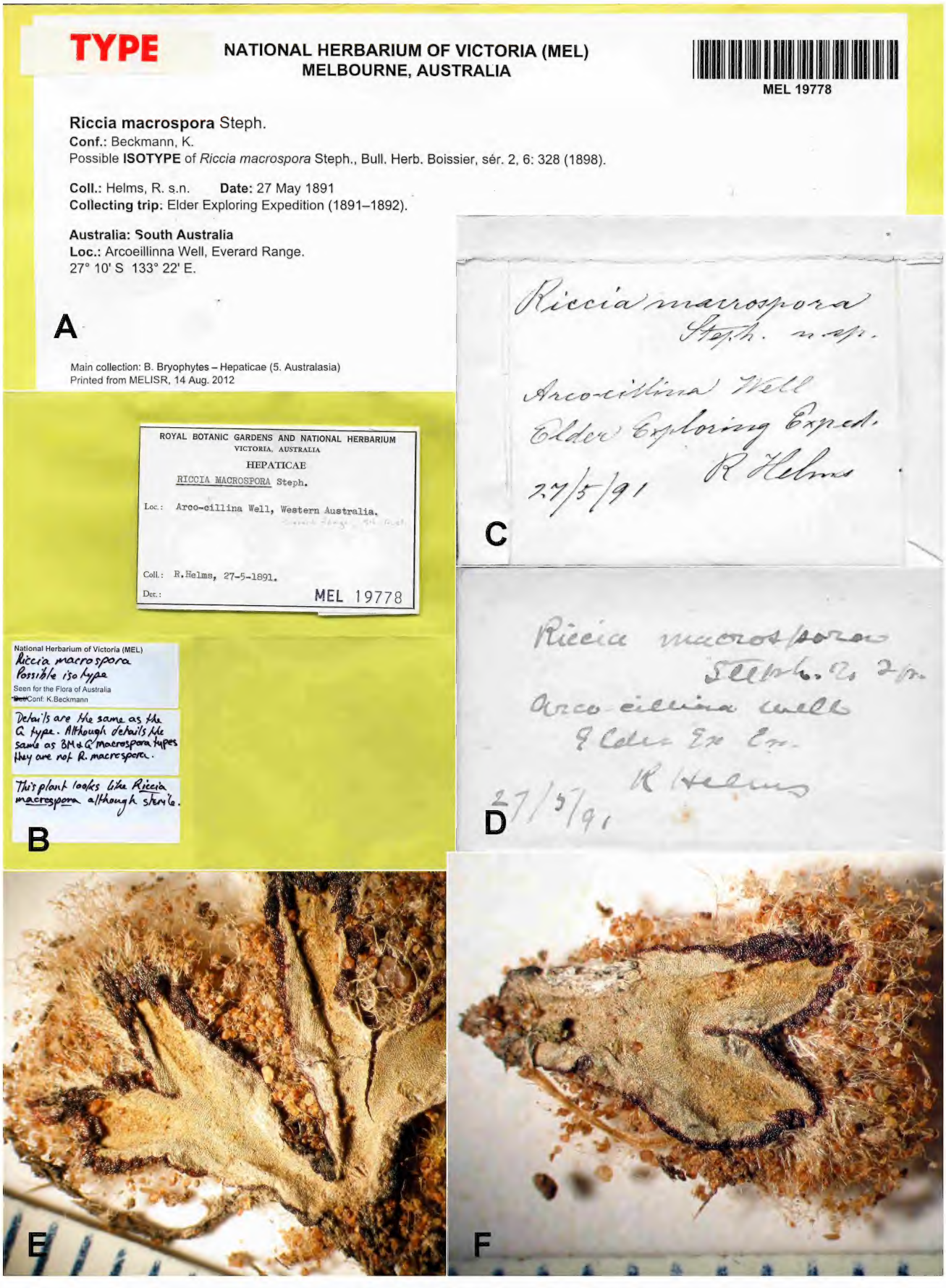

Fig. 6. *Riccia macrospora* syntype (MEL). **A–D** Packet, labels and determination slips associated with specimen. **E, F** Close up of specimen plants (scale divisions = 1 mm). — Permission is given by the Royal Botanic Gardens Victoria (RGBV) to publish the images taken by D.C. Cargill of MEL's syntype specimen, MEL19778.

Fig. 7. *Riccia macrospora* syntype (AD). Herbarium specimen comprising labelled packet at top and contents below. — Image courtesy of the State Herbarium of South Australia, Botanic Gardens and State Herbarium, Department for Environment and Water, South Australian Government.

reticulate and resembling a cogwheel in optical section, not unlike the spores typically seen in *R. billardierei* Mont. & Nees or *R. discolor* Lehm. & Lindenb. This is at variance with the spores of the lectotype at G (Fig. 2C–E) and the drawing made by Stephani in his *Icones* (Fig. 1). Na-Thalang's concept of *R. macrospora* appears to be based on Stephani's description and the examination of types of two species she synonymised under *R. macrospora*: *R. runssorensis* Steph. from central Africa and *R. sellingii* S.W.Arnell from central Australia. She states: "From an examination of the type material of *R. runssorensis* Steph. and *R. sellingii* [S.W.]Arnell, both appear to be the same plant and have the same characters as *R. macrospora*." (Na-Thalang 1980). She also synonymised an Australian species, *R. rubrispora* Steph. under *R. macrospora* based on the original Stephani description (Stephani 1900) and illustrations (*Icones*) but noting that the type could not be found (Na-Thalang 1980). Since then, the lectotype and isotype have been located at G and BM, respectively.

While Na-Thalang lists the lectotype of *Riccia macrospora* at G (as the 'holotype') and the material at AD (as an 'isotype'), she does not specifically discuss examination of this material, nor its morphology, and only Stephani's description of *R. macrospora* is discussed. The concept used by Seppelt (1974)[5] was based on examination of the type of *R. macrospora* (given as accession number G16101, not the lectotype accession number designated by G and cited by Na-Thalang

5 Seppelt (1974) is a Master's degree thesis and is not effectively published (see Turland *et al.* (2018), Art 30.9). His citations of "Holotype" and "Isotype" specimens therefore do not constitute inadvertent lectotypification of *R. macrospora*.

Fig. 8. *Riccia macrospora* syntype (AD). **A** Portion of specimen contents showing plants and labels. **B, C** Individual plants showing bright crimson-maroon scales extending beyond the thallus margins. — Images courtesy of the State Herbarium of South Australia, Botanic Gardens and State Herbarium, Department for Environment and Water, South Australian Government.

Fig. 9. *Riccia macrospora* isolectotype (BM) comparing ventral scales. **A** Portion of the dried herbarium specimen (scale = 1 mm). **B–D** Magnified images of plants showing the darkly pigmented scales around the margins and along the ventral flanks. — BM000824105 & BM000824106 from the collections of the Natural History Museum, London with permission to use images of specimen. Photos taken by D.C. Cargill.

(1980); this is probably a typographic error: G16101 is the type specimen of *R. macropora* (Steph.) Steph. from Paraguay; pers comm. Isabella Valette, Herbarium Secretary, Cryptogamic herbarium, Conservatoire et Jardin botaniques, Geneva, 13 May 2019). The type label information given, however, is the same and it is clear that he agreed with Na-Thalang's concept by confirming the synonymy of *R. rubrispora* under *R. macrospora* (Seppelt 1998).

While separate species status for *Riccia macrospora* is supported, its placement by Na-Thalang (1980) in a species group including the northern Australian taxa *R. billardierei*, *R. discolor* and *R. gangetica* Ahmad ex L.Soderstr., A.Hagborg & von Konrat, is misleading. *Riccia macrospora* is morphologically more similar to the southern Australian *R. inflexa*, with which it shares the scales extending beyond the thallus margins, winged spores with three pores and a more or less reticulate spore patterning. When scales are rehydrated, however, *R. inflexa* scales differ in colour, and are always purplish and pigmented throughout the scale, as compared to crimson to purplish-violet, with the pigmentation often confined to the margins of the scale with the basal area hyaline in *R. macrospora*.

Riccia macrospora has previously been treated as a taxon confined to northern South Australia and the southern part of the Northern Territory (Seppelt 1974, 1998; Na-Thalang 1980). However, examination of collections at CANB, following clarification of the application of the name, indicates that *R. macrospora*

TYPE
NATIONAL HERBARIUM OF VICTORIA (MEL)
MELBOURNE, AUSTRALIA
MEL 19778
Riccia macrospora Steph.
Conf.: Beckmann, K.
Possible ISOTYPE of Riccia macrospora Steph., Bull. Herb. Boissier, sér. 2, 6: 328 (1898).
Coll.: Helms, R. s.n. Date: 27 May 1891
Collecting trip: Elder Exploring Expedition (1891–1892).
Australia: South Australia
Loc.: Arcoeillinna Well, Everard Range.
27° 10' S 133° 22' E.
A
Main collection: B. Bryophytes – Hepaticae (5. Australasia)
Printed from MELISR, 14 Aug. 2012
B
5 mm
C
D
1 mm

Fig. 10. *Riccia macrospora* syntype (MEL) comparing ventral scales. **A** Front of herbarium packet showing label of MEL specimen. **B–D** Individual plants showing large scales curling over the margins of the segments. — Permission is given by the RBGV to publish the images taken by D.C. Cargill of MEL's syntype specimen, MEL19778.

is more widespread than previously thought. Based on existing collections at CANB, *R. macrospora* also occurs in Queensland, from the Cook district south to the Darling Downs district west of Brisbane. Further collecting and examination of additional collections in other herbaria will likely expand the distribution of *R. macrospora* further.

The name *Riccia limbata* (misapplied by Na-Thalang 1980 to the southern Australian taxon *R. inflexa*) has also been misapplied to collections of *R. macrospora* in Australian herbaria. *Riccia limbata* is a southern African taxon, not known to occur in Australia and may be distinguished from *R. macrospora* by the patterning of its spores. *Riccia limbata* spores possess a 'swirl' pattern

of lamellae on the distal face, sometimes found on spores in *R. macrospora* (Fig. 5C), however it is the proximal face that differs significantly. The proximal face of *R. limbata* bears small, regular fovea punctuating an otherwise smooth surface (Perold 1999). *Riccia macrospora* on the other hand has alveoli which are large, irregular in size and shape and surrounded by a vermiculate-like border (Fig. 5D, F).

Nomenclature

***Riccia macrospora* Steph.**, *Bull. Herb. Boiss.* 6: 20 (1898).

Type citation: "*Australia centralis*. Arco-eillinna well. Elder Explor. Exped. (Helms)". **Lectotype:** Arco-ellina [Arcoeillina] Well, 27 May 1891, *R. Helms s.n.* (G000526000, old accession no. 12730), *fide* Na-Thalang, *Brunonia* 3: 86 (1980), as "Holotype" (correctable under ICN Art. 9.10; Turland *et al.* 2018). **Isolectotype:** BM000824105 & BM000824106. **Excluded syntypes:** AD-C12604 (cited by Na-Thalang as "AD 19"); MEL19778.

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Three species of *Cryptandra* (Rhamnaceae: Pomaderreae) from southern Australia allied to *C. tomentosa*

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Abstract: Two species of *Cryptandra* are described as new, *C. setifera* Kellermann and *C. sabulicola* Kellermann, and *C. campanulata* Schltdl. is formally reinstated. The species are described and illustrated, synonymies are provided, as well as an identification key for the *C. amara-tomentosa* complex in Victoria and South Australia. Specimens of all three taxa have formerly been identified as *C. amara* Sm. or *C. tomentosa* Lindl., but are clearly separate from them.

Keywords: New species, Rhamnaceae, *Cryptandra*, South Australia, Victoria

Introduction

Cryptandra Sm. is a genus of about 60 species, mainly distributed in southern Western Australia and south-eastern Australia, with a few species occurring in the north of the continent. During the last 25 years, research on the genus was undertaken in Western Australia (Rye 1995, 2007; Rye & Trudgen 1995), Queensland (Bean 2004) and Victoria (Walsh & Udovicic 1999). The genus is currently being revised over its whole range of distribution, which has already resulted in the publication of new taxa (Kellermann 2006a, b; Kellermann & Udovicic 2007) and nomenclatural notes and typifications (Kellermann & Rye 2008).

During work on the *C. amara-tomentosa* complex, three taxa were recognised as morphologically distinct. This result was corroborated by preliminary molecular analyses of the tribe Pomaderreae (see Nge *et al.* 2019 & in press.). In this paper, two taxa are described as new and one is formally reinstated. All three species have been variously assigned to *C. amara* Sm. or *C. tomentosa* Lindl. over the years. A full resolution of the variation within *C. amara* and *C. tomentosa* is still being worked on, but the taxonomic changes published here are presented in advance so that names for the species are available. The presence of *C. myriantha* Diels in South Australia and Victoria was confirmed by Kellermann & Rye (2008); it is included in the key, below, as it can be confused with *C. tomentosa*.

The first new species, *Cryptandra setifera* Kellermann, is restricted to rocky habitats in the north of Eyre Peninsula, South Australia, extending to the Gawler Ranges. The second new species, *C. sabulicola* Kellermann, is native to deep sands in northern Eyre Peninsula and on both sides of the South Australian-Victorian border, especially in and around Billiat Conservation Park (C.P.), Murray-Sunset National Park (N.P.) and the Big Desert. *Cryptandra campanulata* Schltdl. grows in rocky habitats of the northern Mount Lofty Ranges and southern Flinders Ranges.

Materials & Methods

This study is based on herbarium specimens from AD, CANB, HO, MEL and NSW, as well as field observations and freshly collected material. Vegetative characters and fruits were measured from dry specimens; floral features were mainly taken from rehydrated material, but also from material preserved in 70% ethanol. The type specimen of *Cryptandra campanulata* was examined on JSTOR (2020).

Taxonomy

1. *Cryptandra setifera* Kellermann, *sp. nov.*

A Cryptandra campanulata *Schltdl. stipulis setosis adaxialibus, floribus brevibus, et fructibus toris medialis differt.*

Holotypus: South Australia, Eyre Peninsula: Property of Bill & Kerry Campbell, hillside S of Urbana Weir Road, c. 250 m from road, NW facing slope, open woodland with *Allocasuarina*, *Acacia*, *Eucalyptus* & *Dodonaea*, red loamy sand over quartzite rock with exposed rock sheets and boulders, 1 m tall spiny shrub, branches entangled, 23 Oct. 2018, *J. Kellermann 750 & F. Nge* (AD285099). **Isotypi:** B, CANB, HAL, K, MEL, MO, NY, SI.

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Cryptandra sp. Hiltaba (*Anon. NPGA-8100*) Kellermann in Lang *et al.*, *Fl. Surv. Hiltaba Station & Gawler Ra. Natl Park* 35–36, Figs 25, 26 (2013); Austral. Biol. Resources Study, *Hiltaba Nat. Res. & Gawler Ra. Natl Park 2012 Bush Blitz Surv.* 30 (2015).

Cryptandra amara auct. non Sm.: J.M.Black, *Fl. S. Austral. ed. 2*, 3: 552 (1952), *pro parte*.

Cryptandra amara var. *floribunda auct. non* Maiden & Betche: J.M.Black, *Fl. S. Austral. ed. 2*, 3: 552 (1952), *pro parte*; E.M.Canning in Jessop & Toelken, *Fl. S. Austral.* 2: 808 (1986), *pro parte*.

Cryptandra sp. Floriferous (*W.R.Barker 4131*) *auct. non* W.R.Barker: W.R.Barker, *J. Adelaide Bot. Gard. Suppl.* 1: 90 (2005), *pro parte*.

Shrubs, 0.3–1.2 m high, with abundant spinescent short-shoots. *Indumentum* on young stems of dense stellate and simple hairs, white, stems soon becoming glabrous. *Stipules* (0.4–) 1–2.8 mm long, persistent, narrowly to broadly triangular, acute to attenuate, long-acuminate with a long drawn-out ± curly tip when young, connate at the base of the petiole, glabrous or sparsely hairy abaxially (outside), adaxially with dense long coarse simple hairs or bristles, ciliate, light brown when young, later darker; *petiole* (0.1–) 0.4–1.1 mm long, glabrous. *Leaves* alternate or in fascicles, shortly petiolate; *lamina* narrowly ovate to linear, entire, 1.3–5 (–7) mm long, 0.3–1 mm wide; base cuneate to obtuse; margins revolute (almost terete); apex acute to bluntly acuminate, straight (rarely incurved); abaxial (lower) surface obscured by margins, densely stellate hairy, with stellate or simple hairs along midrib; adaxial surface glabrous or with very short fine erect simple hairs. *Inflorescences* axillary, comprising single flowers surrounded at base by 6–9 bracts, arranged in little-branched ± elongate conflorescences of up to 20 flowers. *Bracts* persistent, ovate to orbicular, 1.3–2.3 mm long, brown, obtuse to acute, sparsely pubescent, especially in upper half; margins entire or torn and ragged, ciliate. *Flowers* white, sessile; *hypanthium* shortly tubular, 1–1.5 mm long, 2.3–2.9 mm in diameter, covered outside with sparse to moderately dense antrorse simple hairs overlying dense small stellate hairs; base with dense stellate hairs. *Sepals* 1.8–2.1 mm long, erect, keeled, persistent on fruit, with a similar indumentum as hypanthium. *Petals* 0.8–1.0 mm long, erect, cucullate, ± clawed. *Stamens* 0.7–1 mm long, shorter than or subequal to petals, erect to incurved; *anthers* 0.3–0.5 mm long. *Disc* inconspicuous, forming a narrow ring around the ovary, densely stellate-pubescent. *Ovary* inferior to almost so; roof densely pubescent with stellate hairs; *carpels* 3; *style* 1–1.6 mm long, glabrous, shortly 3-lobed. *Fruit* a schizocarp, obovoid to ellipsoid, 2.7–3.5 mm long, brown with white to grey indumentum; torus in middle third; *fruitlets* dehiscing by a longitudinal slit on the inner face. *Seeds* 1.7–1.8 mm long, dark fawn to light brown, uniformly coloured, darker at base; *aril* c. 0.4 mm long, at base of seed, pale yellowish, translucent. **Fig. 1.**

Preliminary key to the *Cryptandra amara-tomentosa complex* in Victoria and South Australia

1. Leaves mostly flat, glabrous on both sides apart from a few simple hairs along the midrib . . . . . ***C. amara***

1: Leaves recurved to revolute, glabrous above (sometimes muricate, especially on the distal half of the leaf), densely tomentose below

2. Leaf apex conspicuously recurved, plants without spinescent short shoots . . . . . 2. ***C. sabulicola***

2: Leaf apex straight, plants spinescent or not

3. Flower with hypanthium tube > 2.5 mm long, with 5 ridges along the tube, covered in dense stellate and simple hairs; torus ± basal in fruit . . . . . 3. ***C. campanulata***

3: Flower with hypanthium tube < 2 mm long, not or scarcely ridged, moderately to densely pubescent to glabrous; torus in middle of fruit

4. Stipules to 2.8 mm long, with a long drawn-out curly tip when young (later breaking off), glabrous abaxially (outside), with dense coarse simple hairs present on adaxial surface; plants densely spinescent . . . . . 1. ***C. setifera***

4: Stipules to 2 mm long, acute to acuminate, but not long drawn-out when young, usually with hairs abaxially, especially in centre, glabrous or sparsely hairy adaxially; plants spinescent or not

5. Hypanthium tube with persistent indumentum on tube and base; indumentum of stems and flowers of stellate hairs overlain by simple hairs . . . ***C. tomentosa* var. 2 = *C.* sp. Floriferous (*W.R.Barker 4131*)**

5: Hypanthium tube glabrous or glabrescent, at least toward base

6. Indumentum on stems and flowers usually of moderately dense to dense minute stellate hairs, occasionally with simple hairs; hypanthium tube fully glabrous or glabrous at base, at least in fruit . . . . . ***C. tomentosa* var. 1 = *C. tomentosa s.str.***

6: Indumentum on stems of strigose simple hairs, early glabrescent; hypanthium tube fully glabrous; sepals with sparse to medium short antrorse simple hairs, very occasionally with stellate hairs . . . . . ***C. myriantha***

Fig. 1. *Cryptandra setifera* growing in rocky hills near Urbana Weir Road, near Cleve and Calwell, Eyre Peninsula (type locality). **A** Habit. **B** Flowering branchlet with long spinescent short-shoot. — A *J. Kellermann 751 & F. Nge*, B *JK 750 & FN*. Photos by J. Kellermann.

Illustrations: Lang *et al.*, *Fl. Surv. Hiltaba Station & Gawler Ra. Natl Park* 37, Figs 25, 26 (2013), photographs, as *Cryptandra* sp. Hiltaba.

Distribution and habitat. *Cryptandra setifera* occurs in rocky, sometimes skeletal soils, mainly over quartzite or granite, rarely on sandstone or limestone, on rocky outcrops and with cobble strew. It grows in heath and scrubland on hills and higher altitudes of northern Eyre Peninsula from the western Gawler Ranges to Port Augusta, with two records from as far east as Wilpena Pound in the Flinders Ranges (Fig. 5).

Phenology. Flowers June–Nov.; fruits Aug.–Nov.

Distinguishing characters. The species is unique in the *C. amara-tomentosa* complex in having dense long coarse hairs or bristles on the inside of the stipules. While hairs on the inside of the stipules occur in other species (e.g. *C. sabulicola*, below), the hairs in *C. setifera* are much longer, coarser and denser than in other taxa. In its fiercely spinescent habit, the species is similar to *C. campanulata*, but that taxon grows not as tall and differs in having very long-tubular flowers with five ridges and fruits with a basal torus (vs. shorter flower tubes and a torus in the middle third of the fruit).

Notes. The taxon was first segregated during earlier work on the *Cryptandra amara-tomentosa* complex under the tag name '*Cryptandra* hairy armpits', in reference to the hairs on the back of the stipules, and some specimens in several herbaria are labelled as such. It was also collected during the 2012 Bush Blitz expedition to Hiltaba Station and the western Gawler Ranges (Lang *et al.* 2013; Bush Blitz 2015), where it was assigned the phrase name *Cryptandra* sp. Hiltaba (*Anon. NPGA-8100*) Kellermann.

Conservation status. The species is found in several reserves in the northern half of Eyre Peninsula, including the Gawler Ranges N.P. and Carappee Hill C.P. It also grows in private conservation areas like Hiltaba and Secret Rocks Nature Reserves (Lang *et al.* 2013; DEWNR 2014). Its conservation status should be assessed.

Etymology. From the Latin *setifer* (bearing bristles), in reference to the coarse hairs on the inner surface of the stipules.

Selected specimens examined (over 120 seen)

SOUTH AUSTRALIA. Paney Stn, quadrat four, [Gawler Ranges Survey,] 10 Oct. 1985, *Anon. NGPA-7682* (AD); Hiltaba Stn, Hiltaba site, quadrat four, [Gawler Ranges Survey,] 25 Oct. 1985, *Anon. NGPA-8100* (AD); Uno Range, 8 Nov. 1979, *P.E. Conrick 205* (AD); Kyancutta, 26 Aug. 1969, *B. Copley 2602* (AD); c. 40 km W of Iron Knob and c. 10 km SE of Siam Stn, 15 Aug. 1967, *M. Fagg 397* (AD); SW side of Hummock Hill, E end of Whyalla, 11 June 2006, *C. Garrett s.n.* (AD193660); Pile Pudla Res., hill E of picnic

ground, on top of hill, west facing slope, near quartzite ridge, 18 Oct. 2018, *J. Kellermann 664 & F. Nge* (AD, MEL, NSW); Property of B. & K. Campbell, hillside south of Urbana Weir Road, c. 250 m from road, NW facing slope, 23 Oct. 2018, *J. Kellermann 751 & F. Nge* (AD); Just S of summit [of] hill on ridge SW of Peeweena Bore, Hiltaba Stn, 14 Nov. 2012, *J. Kellermann, P.J. Lang & H. Cross BS838-169* (AD, B, BM, CANB, KUN, MEL); 3.5 km W of Old Paney [Homestead], Old Paney–Scrubby Peak [track], 28 July 2001, *F. Kutsche UGGR07/01 84* (AD); 1.1 km direct SSW of Spring Hill, Thurlga Stn, 16 Aug. 2000, *P.J. Lang & L.M.B. Heard BS1-10076*; 4.6 km direct SSW of Mt St Mungo, Hiltaba Stn, 19 Aug. 2000, *P.J. Lang & L.M.B. Heard BS1-10190*; Wilpena Pound, c. 40 km NNW of Hawker, 15 Sep. 1977, *Robinson s.n.* (AD97747723); 5.3 km WSW of Ebunbanie Hill, Yardea Station, 17 Aug. 2000, *A.C. Robinson & L.A. Kajar BS1-10683* (AD); Hundred of Buckleboo, E side of Sec. 70, c. 45 km WNW of Kimba, 2 Aug. 1959, *K.D. Rohrlach 372* (AD; B, L *n.v.*); On Peterlumba and near vicinity Buckleboo Stn, 15 Aug. 1959, *K.D. Rohrlach 420* (AD; BM, K *n.v.*); S side of Carappee Hill (reserve), c. 35 km SW of Kimba, 30 Aug. 1959, *K.D. Rohrlach 463* (AD; K *n.v.*); Middleback Range, NE of Iron Dutchess, 20 Sep. 1981, *D.J.W. Whibley 7682* (AD).

2. *Cryptandra sabulicola* Kellermann, *sp. nov.*

A Cryptandra recurva *Rye foliis glabris longioribusque, fructibus et seminibus largioribus differt.*

Holotypus: South Australia, Murray: Dingo Range, ca. 32 km NW of Pinnaroo [Pinnaroo is ca. 142 km E of Murray Bridge], 31 Aug. 1961, *N.N. Donner 282* (AD96211242). **Isotypi:** B, CANB, K, KW, MEL, MO, NY, SI.

Cryptandra amara var. *floribunda auct. non* Maiden & Betche: J.M.Black, *Fl. S. Austral. ed. 2*, 3: 552 (1952), *pro parte*.

Cryptandra tomentosa auct. non Lindl.: J.M.Black, *Fl. S. Austral.* 3: 370 (1926), *pro parte*; *ed. 2*, 3: 551 (1952), *pro parte*; J.H.Willis, *Handb. Pl. Victoria* 2: 372 (1973), *pro parte*; E.M.Canning in Jessop & Toelken, *Fl. S. Austral.* 2: 810 (1986), *pro parte*.

Cryptandra tomentosa var. 2: N.G.Walsh & Udovicic, *Fl. Victoria* 4: 112 (1999), *pro parte*.

Cryptandra sp. Floriferous (*W.R.Barker 4131*) *auct. non* W.R.Barker: W.R.Barker, *J. Adelaide Bot. Gard. Suppl.* 1: 90 (2005), *pro parte*.

Shrubs, 0.3–1.2 m high, without spinescent short-shoots. *Indumentum* on young stems of dense stellate and simple hairs, white to rusty, stems becoming glabrous when older. *Stipules* (0.6–) 1–2.6 (–3.6) mm long, persistent, narrowly to broadly triangular, acute (some attenuate), connate at the base of the petiole, glabrous to moderately hairy abaxially (outside), adaxially with a few simple hairs, sparsely ciliate, brown; *petiole* 0.1–0.6 mm long, glabrous, some with stellate hairs on the abaxial side. *Leaves* alternate or in fascicles, shortly petiolate; *lamina* narrowly ovate to linear to narrowly obovate, entire, 2–5 mm long, 0.4–1.1 mm wide; base cuneate to obtuse; margins revolute; apex acute to acuminate, strongly recurved; abaxial surface largely obscured by margins, densely stellate-hairy with some simple hairs, with stellate and longer simple hairs along midrib; upper surface glabrous to sparsely muricate (especially on the distal half of the leaf). *Inflorescences* axillary or terminal, comprising single flowers surrounded at base by c. 5 bracts, arranged in little-branched ± elongate conflorescences of up to 20 flowers. *Bracts* persistent, ovate to orbicular, 1–1.2 mm long, brown, obtuse, glabrous to pubescent; margins entire or torn and ragged, ciliate. *Flowers* white, sessile; *hypanthium* shortly tubular, 0.5–0.8 mm long, 1.8–2.6 mm in diameter, covered with sparse to moderately dense antrorse simple hairs overlying dense small stellate hairs; base similarly pubescent. *Sepals* 1–1.5 mm long, erect (rarely spreading), keeled, persistent on fruit, with a similar indumentum as hypanthium. *Petals* 0.6–0.9 mm long, erect to incurved, cucullate, distinctly clawed. *Stamens* 0.6–0.8 mm long, shorter than or subequal to petals, erect to incurved; *anthers* 0.2–0.3 mm long. *Disc* inconspicuous, forming a narrow ring around the ovary, densely stellate pubescent. *Ovary* inferior to almost so; roof densely pubescent with stellate hairs; *carpels* 3; *style* 0.7–1 mm long, glabrous, shortly 3-lobed. *Fruit* a schizocarp, obovoid to ellipsoid, 2.2–3 mm long, brown to yellowish-brown with grey indumentum; torus in middle to upper third; *fruitlets* dehiscing by a longitudinal slit on the inner face. *Seeds* 1.5–1.8 mm long, fawn to light brown, uniformly coloured, darker at base; *aril* c. 0.9 mm long, at base of seed, pale yellowish, translucent. **Figs 2, 3E–I.**

Distribution and habitat. *Cryptandra sabulicola* occurs in deep sandy soils on sand hills, sand dunes and swales, in mallee vegetation, heath and scrubland in the northern half of Eyre Peninsula, from Yumbarra C.P. to Pinkawillinie C.P. and Munyaroo C.P., in the Murray mallee in South Australia, especially in and around the Billiat Wilderness Protection (W.P.A.) and the adjacent Murray-Sunset N.P., Wyperfeld N.P., Big Desert Wilderness Park and Big Desert State Forest in Victoria, as far east as Hattah-Kulkyne N.P. (Fig. 5).

Phenology. Flowers Aug.–Oct.; fruits Oct.–Nov.

Distinguishing characters. The species can be immediately recognised within the *C. amara-tomentosa* complex by its recurved leaf apices. In Victoria and South Australia it can be confused with *C. tomentosa* var. 2 (Walsh & Udovicic 1999), which has similar flowers, but that species has straight leaves.

The Western Australian *C. recurva* Rye also has strongly recurved leaf apices, but is a smaller shrub and the adaxial leaf surface is densely pubescent with minute stellate hairs and appears grey-green, compared to the green, glabrous to sparsely muricate adaxial leaf surface in *C. sabulicola*. A few specimens of *C. recurva* have glabrous leaves, but these are consistently smaller (2–3.8 mm long, 0.5–0.8 mm wide; Rye 1995) and the stipules are also shorter (0.5–1 mm long). In addition,

Fig. 2. *Cryptandra sabulicola* in the Big Desert, Victoria (A, D), and Billiat Wilderness Protection Area, South Australia (B, C). **A** Shrub growing in deep sand. **B** Branchlet with buds, showing leaves with recurved apices. **C** Flowering branches. **D** Close up of flowers. — A *J. Kellermann 915 & F. Nge*, B *JK 795 & FN*, C *JK 905 & FN*, D *JK 908 & FN*. Photos by J. Kellermann.

fruits and seeds of *C. sabulicola* are larger than in *C. recurva* (which has fruits 2–2.5 mm long and seeds 1.3–1.5 mm long).

Notes. As plants with recurved leaf apices have not been recognised as distinct in the past, specimens of *Cryptandra sabulicola* were variously identified as *C. amara* or *C. tomentosa* or varieties of these two species. During the last 15 years, I have labelled specimens in several Australian herbaria as '*Crytandra* recurved apex'.

Conservation status. The species is locally common in areas with deep sand and is conserved in several parks and reserves, as listed above. Its conservation status should be assessed.

Etymology. From the Latin *sabulum* (sand) and *-cola* (dweller), as the species is restricted to sandy soils.

Selected specimens examined (over 100 seen)

SOUTH AUSTRALIA. Yumbarra C.P., 4 Sep. 1984, *D. Keane 25* (AD, BRI); Pinkawillinie C.P., Stringer Hwy, S side of road, c. 100 m west of park boundary, 19 Oct 2018, *J. Kellermann 679 & F. Nge* (AD, MEL, PERTH); Intersection of Bell/Broadbent/Hen and Chicken/Wilke Roads, 23 Oct. 2018, *J. Kellermann 756 & F. Nge* (AD, BM); Les Franklin Road, c. 1 km S from Guidera Road, 23 Oct. 2018, *J. Kellermann 769 & F. Nge* (AD, CANB, NSW); Bakara C.P., track into Park, E of Start Road, 26 Aug. 2019, *J. Kellermann 788 & F. Nge* (AD); Billiat W.P.A., E of Billiat Hwy, 27 Aug. 2019, *J. Kellermann 795 & F. Nge* (AD); Zadow Road, W side, c. 50 m from road, 5 Oct. 2019, *J. Kellermann 904 & F. Nge* (AD, MEL); Billiat W.P.A., W of Billiat Hwy, 50 m from road, *J. Kellermann 905, 906 & F. Nge* (AD; AD, MEL, KUN); Pureba C.P., S boundary on new electric dingo fence, *P.J. Lang BS113-32* (AD); 10.1 km direct WSW of Pinkawillinie, Pinkawillinie C.P., 27 Nov. 2002, *A.C. Robinson & J.T. Mcdonald BS128-1554* (AD); Peebinga C.P. E, 5 Oct. 1992, *A.G. Spooner 13583* (AD); 15 km N of

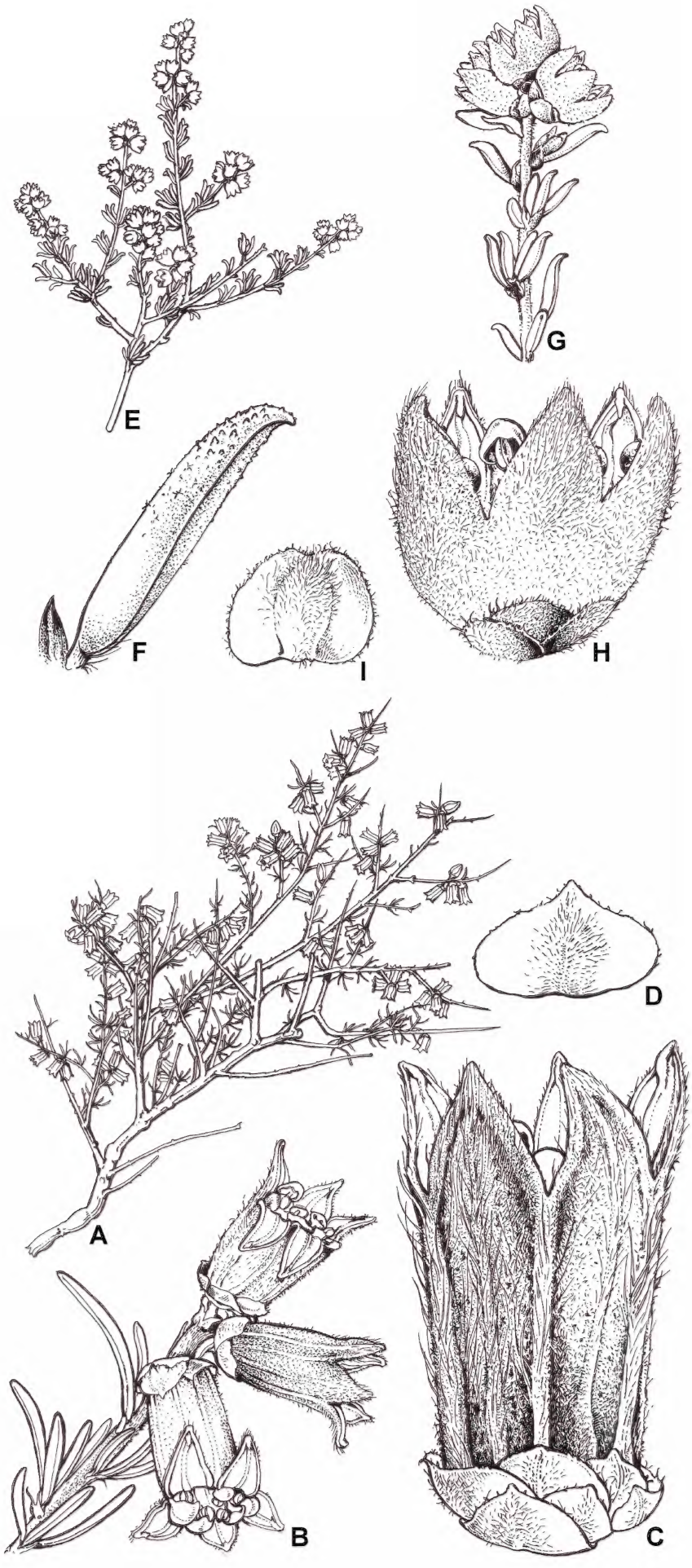

Fig. 3. A–D *Cryptandra campanulata*: **A** Habit ×0.6; **B** flowering branchlet ×4; **C** flower ×13; **D** bract ×10. **E–I** *C. sabulicola*: **E** Habit ×0.6; **F** leaf ×13; **G** flowering branchlet ×4; **H** flower ×13; **I** bract ×10. — A *A.G. Spooner 13242* (AD99233210), B–D *B. Copley 3464* (AD97143260), E *M.G. Corrick 6374* (AD98023206), F–I *D.G. Cameron 8722* (MEL0581322). Illustration by Anita Barley.

Koonibba, c. 35 km NW of Ceduna, 11 Sep. 1960, *D.J.E. Whibley 587* (AD; UC *n.v.*)
VICTORIA. Wyperfeld N.P., c. 1 mile [1.6 km] S of Moorong Rise, 12 Nov. 1968, *A.C. Beauglehole 29531* (AD, MEL); Vicinity of junction of Murray Valley Hwy and park entrance road, Hattah-Kulkyne N.P., 30 Aug. 1977, *D.G. Cameron 8722* (AD, MEL, NSW); Big Desert, 13 km S of Murrayville on road to Nhill, Oct. 1979, *M.G. Corrick 6374* (AD, MEL); Murray-Sunset National Park, SW corner, NE of intersection with Bellbird Bore Road and S boundary track, on top of sand dune, 5 Oct. 2019, *J. Kellermann 907, 908 & F. Nge* (AD, MEL; AD, MEL, NSW); Big Desert, 10 m W of Murrayville-Nhill Road, 13 km South of Murray Hwy, flat between dunes, 6 Oct. 2019, *J. Kellermann 915 & F. Nge* (AD, MEL); Annuello Flora and Fauna Res., *s. dat., J.N. MacFarlane 3498* (MEL); Last Hope Track, approx. S of Spectacle Lake, 20 Sep. 2014, *R.W. Purdie 9610* (MEL; CANB *n.v.*).

3. *Cryptandra campanulata* Schltdl.

Linnaea 20: 639–640 (1847). — **Type citation:** "Vom steinigen Ostabhange des Gebirges gegen den Murray-Scrub". **Holotype:** South Australia, Northern Lofty: Vom steinigen Ostabhange des Gebirges gegen den Murray scrub, July, *s.anno* [1845], *H.H. Behr s.n.* [156] (HAL0098383, photo seen), *fide* B.Heuchert *et al.*, *Schlechtendalia* 31: 49 (2017).

Cryptandra amara auct. non Sm: Benth., *Fl. Austral.* 1: 440 (1863), *pro parte*.

Cryptandra amara var. *longiflora auct. non* F. Muell. ex Maiden & Betche: J.M. Black, *Fl. S. Austral.* 3: 370 (1926); E.M. Canning in Jessop & Toelken, *Fl. S. Austral.* 2: 808 (1986).

Cryptandra sp. Long hypanthium (*C.R. Alcock 10626*) W.R. Barker, *J. Adelaide Bot. Gard. Suppl.* 1: 90 (2005).

Shrubs, 0.3–1 m high, spinescent. *Indumentum* on young stems of dense stellate and occasional simple hairs, white-greyish, sometimes rusty, stems soon becoming glabrous. *Stipules* (0.4–) 1–1.9 mm long, persistent, narrowly triangular to linear-filiform, acute to attenuate, connate at the base of the petiole, glabrous or sparsely hairy abaxially (outside), adaxially glabrous, light brown when young, later dark brown; *petiole* (0.1–) 0.2–0.7 (–1) mm long, stellate-pubescent. *Leaves* alternate or in fascicles, shortly petiolate; *lamina* narrowly elliptic to narrowly ovate to linear, entire, (2–) 2.3–5.5 (–8) mm long, 0.3–0.7 mm wide; base

Fig. 4. *Cryptandra campanulata* growing in Mokota Conservation Park (A, B) and near Black Springs (C), South Australia. **A** The species as major component of iron-grass grassland. **B** Flowering spinescent branches. **C** Close up of flowers. — A, B *J. Kellermann 983 & L. Williams*, C *JK 981 & LW*. Photos by J. Kellermann.

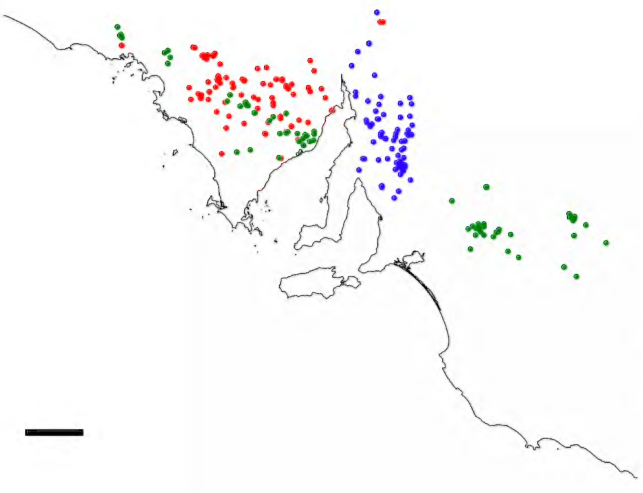

Fig. 5. Distribution map of *Cryptandra setifera* (red), *C. sabulicola* (green) and *C. campanulata* (blue) in southern Australia, from herbarium specimens examined. Scale bar = 100 km.

narrowly cuneate to cuneate; margins revolute to recurved; apex acute or apiculate, sometimes blunt, straight or incurved, with a dark brown tip; abaxial surface obscured by margins, densely stellate-hairy, with stellate or simple hairs along midrib; adaxial surface glabrous to tuberculate. *Inflorescences* axillary, comprising single flowers surrounded at base by 6–8 bracts, arranged in little-branched ± elongate conflorescences of up to 20 flowers. *Bracts* persistent, broadly ovate, orbicular or broadly cordate, 1.2–2 mm long, brown, obtuse to acuminate, entire, ± ciliate, glabrous to sparsely pubescent, especially in centre. *Pedicel* 0.2–1.2 mm long, densely pubescent. *Flowers* white; *hypanthium* long-tubular, 2.8–4.3 mm long, 2.3–3.2 mm in diameter, with distinct ridges along the tube between the sepals, covered with sparse to moderately dense antrorse simple hairs overlying medium to dense small stellate hairs; base similarly pubescent. *Sepals* 1.4–2.2 mm long, erect or slightly spreading, keeled, persistent on fruits, with a similar indumentum as hypanthium. *Petals* 0.8–1.2 mm long, erect, cucullate, not or indistinctly clawed. *Stamens* 0.6–1.1 mm long, shorter than or subequal to petals, erect; *anthers* 0.4–0.7 mm long. *Disc* inconspicuous, forming a narrow ring around the ovary, densely stellate-pubescent. *Ovary* ± superior; roof densely pubescent with stellate hairs; *carpels* 3; *style* 1.2–2 mm long, glabrous, shortly 3-lobed. *Fruit* a schizocarp, obovoid or ellipsoid, 3–4.3 mm long, brown with grey indumentum; torus in lower third to basal; *fruitlets* dehiscing by a longitudinal slit on the inner face. *Seeds* 2.3–2.6 mm long, dark reddish brown, uniformly coloured, darker at base; *aril* c. 0.5 mm long, at base of seed, pale yellowish, translucent. **Figs 3A–E, 4.**

Illustrations: J.M. Black, *Fl. South Australia* 3: 364, Fig. 161B, C (1926); *ed. 2*, 3: 544, Fig. 702B, C (1952); E.M. Canning in J.P. Jessop & H.R. Toelken, *Fl. South Australia* 2: 809, Fig. 427C (1986); all as *C. amara* var. *longiflora*.

Distribution and habitat. This species grows in shallow soils over rocks such as quartzite, granite, sandstone, limestone or shale, in the southern Flinders Ranges and northern Mt Lofty Ranges. *Cryptandra campanulata* is the most frequently encountered woody species in iron-grass grasslands (Turner 2012); it also occurs in heath and shrubland vegetation (Fig. 5).

Phenology. Flowers May–Nov.; fruits Sep.–Nov.

Distinguishing characters. *Cryptandra campanulata* can be recognised by its abundant spinescent short-shoots and long tubular flowers that have five ridges on the outside (see under *C. setifera* for other distinguishing characters). Bentham (1863) synonymised the species with *C. amara*, however, that species can be readily distinguished from *C. campanulata* by its flat leaves.

Note. The name *C. amara* var. *longiflora* has been previously applied to the species, but that variety from New South Wales is no longer recognised and is now a synonym of *C. amara*. Walsh & Udovicic (1999) stated that "South Australian plants referred to [...] that variety [...] warrant recognition as a distinct entity". For a few years (2005–2011), the phrase name *Cryptandra* sp. Long hypanthium (*C.R. Alcock 10626*) W.R.Barker was used for the species (Barker & Lang 2012).

Cryptandra campanulata was first collected by German naturalist Hans Herrmann Behr in the Barossa Valley around 1845, during his first stay in Australia (Bretag 2016). When he returned to Germany, Behr gave his extensive botanical collections to D.F.L. von Schlechtendal in Halle, who studied and described them in two publications (Schlechtendal 1847, 1848). Heuchert *et al.* (2017) examined the types of all taxa published by Schlechtendal and concluded that the specimen of *Cryptandra campanulata* at HAL can be considered as the holotype, as no other duplicates are known to exist (see also McNeill 2014).

Conservation status. The species is listed as 'Rare' in the South Australian *National Parks and Wildlife Act 1972*. It is found in several reserves, such as Mt Remarkable N.P., Telowie Gorge C.P., Caroona Creek C.P. and Mokota C.P.

Etymology. From the Latin *campanulatus* (bell-shaped), in reference to the large tubular flowers.

Selected specimens examined (over 80 seen)

SOUTH AUSTRALIA. Parnaroo, 20 km E of Ucolta and 30 km E of Peterborough, 17 Sep. 1986, *C.R. Alcock 10626* (AD, B, BAA, BM, CANB, HAL, MEL); Roadside near Bethel, 14 June 1999, *R.J. Bates 52993* (AD, BAA); Caroona Creek C.P., Aug. 2005, *R.J. Bates 65653* (AD); Mt Gullet Creek area, 2 km W of Mt Remarkable N.P., Mambray Creek Stn, 1 May 1983, *G. Coombe 156* (AD); Railway Res. above

Lochiel turnoff on Bute to Snowtown Road, 6 Nov. 1966, *B. Copley 858* (AD; B *n.v.*); 3 miles [4.8 km] E of Blyth, 27 June 1971, *B. Copley 3464* (AD); Flagstaff Road, c. 2.5 km E of Barrier Hwy, N side of road, 8 July 2020, *J. Kellermann 981 & L. Williams* (AD, K); Mokota C.P., NW corner on White Hill Road, near Gate 1, 9 July 2020, *J. Kellermann 983 & L. Williams* (AD, HAL); Freeling cemetery, bushland area on W side, 1.3 km direct ENE Freeling (Post Office), 30 Sep. 1993, *P.J. Lang 2155* (AD, KUN); 0.9 km direct NNE of 'Old Belcunda', c. 300 m off White Hill Road beside small creekline, 31 Oct. 2003, *J.T. Mcdonald & A.R. Graham BS162-498* (AD); 2.1 km direct SSE of Mt Lock summit, 3 Nov. 2004, *N.R. Neagle & P. Mahoney BS162-3028* (AD); Black Springs Hill, 1 Aug. 1992, *A.G. Spooner 13242* (AD); Low hill top by old shearers quarters at Franklyn, 26 July 1991, *D.E. Symon 15075* (AD; CANB, MEL *n.v.*).

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Nomenclatural notes on the *Alphitonia* Group in Australia (Rhamnaceae)

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Abstract: The nomenclature and typification of seven species of *Alphitonia* Reissek ex Endl. and *Emmenosperma* F.Muell. is discussed. These two genera form the "*Alphitonia* Group" together with *Granitites* Rye and *Jaffrea* H.C.Hopkins & Pillon from New Caledonia. Lectotypes are chosen for *E. cunninghamii* Benth. and for the synonyms *A. excelsa* var. *acutifolia* Braid, *A. obtusifolia* R.Br. ex Braid and *A. obtusifolia* var. *tenuis* Braid. The lectotypes of *A. petriei* Braid & C.T.White and *A. philippinensis* Braid are clarified. Three species are illustrated: *A. petriei*, *A. whitei* Braid and *E. cunninghamii*.

Keywords: Nomenclature, typification, second-step lectotype, Rhamnaceae, *incertae sedis*, Australia

Introduction

Rhamnaceae Juss. is a medium-sized plant family with over 1000 species in 64 genera. The current intra-familial classification was devised by Richardson *et al.* (2000b), following the first molecular analysis of the whole family (Richardson *et al.* 2000a). The family is divided into 11 tribes, but several genera have not been placed into a tribe, because the molecular analysis did not provide enough evidence as to their position within the family. Subsequent molecular analyses of Onstein *et al.* (2015) and Hauenschild *et al.* (2016, 2018a), included more taxa and provided further information on relationships within the family; they did not, however, resolve the position of all genera *incertae sedis*.

Four of these genera, *Alphitonia* Reissek ex Endl., *Granitites* Rye, *Emmenosperma* F.Muell., and *Jaffrea* H.C.Hopkins & Pillon, are very closely related (Fay *et al.* 2001; Hopkins *et al.* 2015; Hauenschild *et al.* 2018b) and are here referred to as the "*Alphitonia* Group" (Kellermann 2020). Of the above mentioned large-scale molecular analyses, only that of Hauenschild *et al.* (2018a) included accessions of all four genera and retrieved them as a well-supported monophyletic clade, but the relationships to other tribes and unplaced genera were unresolved due to poor support for the backbone of the phylogeny.

Hopkins *et al.* (2015) and Hauenschild *et al.* (2018b) discuss the morphology and taxonomic history of the *Alphitonia* Group. Species of *Alphitonia* and related genera are evergreen trees and shrubs, growing in tropical to subtropical regions (Fig. 1). Almost all species have a characteristic type of fruit dehiscence: when fruits are ripe, they split open and the pericarp falls off, leaving the seeds (usually 3) remaining attached to the base of the fruit (Fig. 3F, P).

Alphitonia (10–15 species) was published in Endlicher (1840), using Reissek's manuscript name and description. He indicated that *Colubrina excelsa* A.Cunn. ex Fenzl was the only member of the genus, but did not validly publish a combination in *Alphitonia*. The name of the type of the genus, *A. excelsa* (A.Cunn. ex Fenzl) Benth., was published by Bentham (1863).

The only revision of the genus over its whole range of distribution was published by Braid (1925a), who divided it into two sections: these were *Alphitonia* sect. *Alphitonia* (published as *A.* sect. *Tomentosae* Braid, but this name is invalid, as the proposed section contains the type) and *A.* sect. *Glabratae* Braid. Suessenguth (1953) followed Braid in his treatment for *Die Natürlichen Pflanzenfamilien*. Since then, only regional treatments and descriptions of new species have been published. Bean (2010) revised the five species of *Alphitonia* in Australia. Hopkins *et al.* (2015) restricted the genus to species classified by Braid (1925a) in *A.* sect. *Alphitonia*.

Granitites (monotypic) was described by Rye (1996) for an unusual species, *G. intangendus* (F.Muell) Rye, which occurrs on granite outcrops of south-western Western Australia and was previously included in *Pomaderris* Labill. and *Cryptandra* Sm. It is most closely related to *Alphitonia* (Rye 1996; Nikulinsky & Hopper 1999) and is recovered as its sister genus in molecular analyses (Fay *et al.* 2001; Hauenschild *et al.* 2018a).

Emmenosperma (5 species) was erected by Mueller (1862) to accommodate *E. alphitonioides* F.Muell.

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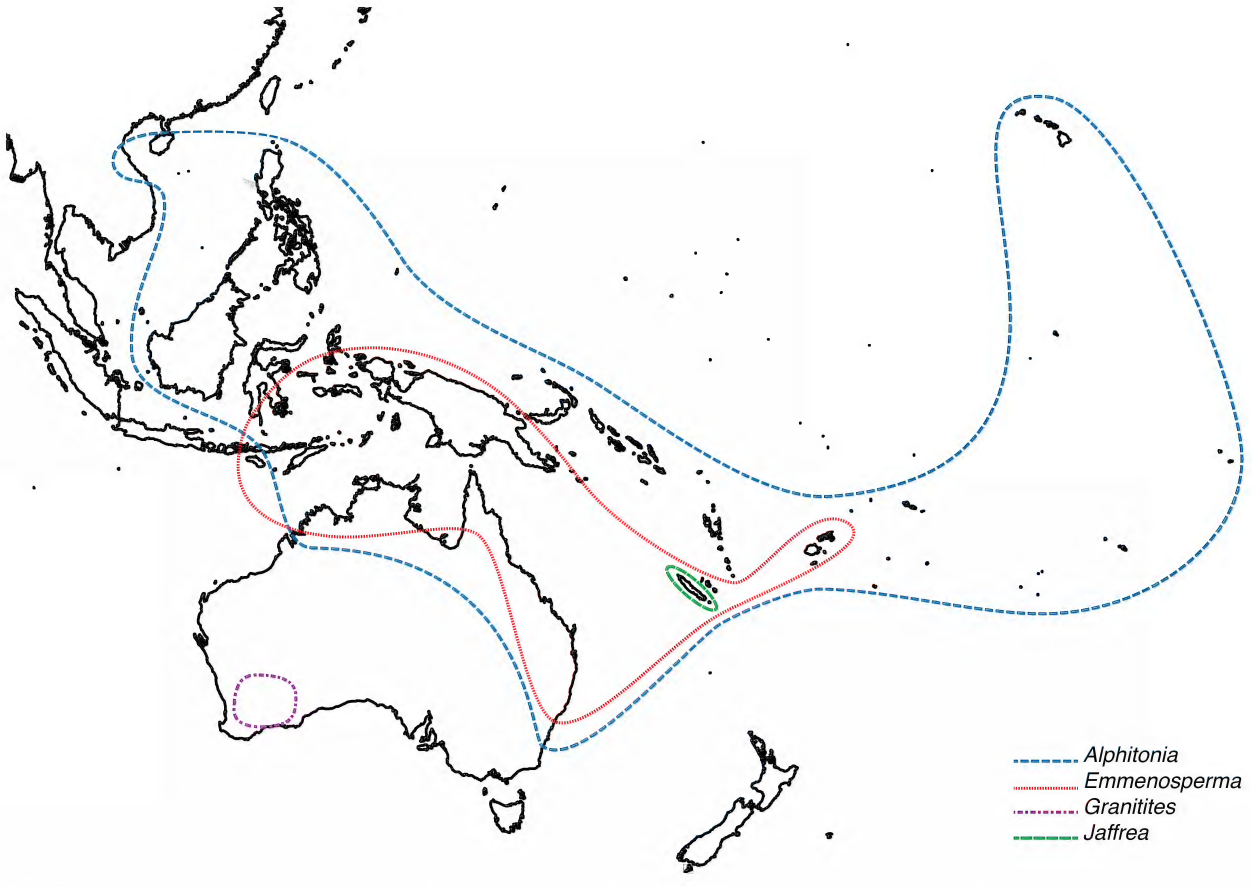

Fig. 1. Distribution of the four genera of the *Alphitonia* Group. Map reproduced from Hopkins *et al.* (2015).

Since then, four other species have been described, but apart from regional treatments, the genus has not been revised; Suessenguth (1953) only provided a short overview of *Emmenosperma*. Two species were known from Australia, until Bean (2013) reported a single population of the New Caledonian taxon *E. pancherianum* Baill. near Townsville in Queensland.

Jaffrea (2 species) was segregated from *Alphitonia* by Hopkins *et al.* (2015) and contains the two species listed by Braid (1925a) in *A.* sect. *Glabratae*, both endemic to New Caledonia. It is the sister genus to *Emmenosperma* (Hopkins *et al.* 2015; Hauenschild *et al.* 2018b). The type species is *J. xerocarpa* (Baill.) H.C.Hopkins & Pillon.

During the preparation of the *Flora of Australia* treatment of Rhamnaceae, it became apparent that the nomenclature of several species of the *Alphitonia* Group in Australia needs to be clarified, especially in the genera *Alphitonia* and *Emmenosperma*. While Bean (2006, 2010, 2013) and Kellermann & Thiele (2008) published some lectotypifications, not all names and their synonyms have so far been typified correctly.

McNeill (2014) clarified some misconceptions about holotypes and procedures for lectotypification and his advice is followed in this paper. All types have been examined; those that were seen online via JSTOR Global Plants and other websites are indicated by "photo seen". In the 1990s, specimens of *Alphitonia* were sent from K on loan to CANB and before they were returned, the sheets were photographed. These images were also available for this study, but as they do not have K barcodes, the specimens are identified by their loan number.

Only species occurring in Australia and taxon names that have been used in an Australian context are reviewed here (APC 2020). Hauenschild *et al.* (2018b) listed type specimens for all names published in the *Alphitonia* Group, but did not suggest taxonomic changes or lectotypifications. Five names are not discussed as they have been typified in the following cited references: *A. oblata* A.R.Bean and the misapplied name *A. incana* (Roxb.) Kurz (typified by Bean 2010), *Emmenosperma alphitonioides* (Kellermann & Thiele 2008), *E. pancherianum* (Bean 2013) and *Granitites intangendus* (Rye 1996).

Three species occurring in Australia are illustrated in Fig. 3: *Alphitonia petriei* Braid & C.T.White, *A. whitei* Braid and *Emmenosperma cunninghamii* Benth.

The *Alphitonia* types of Braid

Kenneth W. Braid was an early adopter of the type-method and indicated and discussed "types" in his taxonomic papers (Braid & Ridley 1924, Braid 1925a, b, c). Although he was working at K at this time, in all but one case (see below), Braid does not state in which

herbarium the type specimen is located, and as such, lectotypification of these names is advisable (McNeill 2014; Mosyakin *et al.* 2019).

In his revision of *Alphitonia*, Braid (1925a: 177) stated that "an asterisk denotes the type specimen, or where material is incomplete the type specimens". For three species, *A. petriei* Braid & C.T.White, *A. whitei* Braid and *A. philippinensis* Braid, he indicated more than one type specimen, i.e. two gatherings are highlighted with an asterisk in the list of collections that were examined. When Bean (2010) lectotypified the first two of these names, he chose specimens of one of the two gatherings that was indicated by Braid.

However, Bean (2010) and other authors overlooked an *addendum* to Braid (1925a), which was published two months after the revision of *Alphitonia* (Fig. 2; Braid 1925b). While no authorship is specified for this *addendum*, it is here assumed that the information was provided by Braid to the journal and he is thus credited with the resulting lectotypifications. Braid explicitly stated that one of the asterisks needs to be deleted in these three species and that the sentence quoted above should be shortened to: "In the following enumeration an asterisk denotes the type specimen", i.e. the reference to multiple types was to be removed.

As such, Braid chose single gatherings as types of these three species of *Alphitonia* in the *addendum*, i.e. he effected the lectotypification of these names. However, since he only designated the gathering, but did not indicate the herbarium in which each gathering is located, this constitutes a first-step lectotypification (Art. 9.17; Turland *et al.* 2018). The selection of a single specimen conserved in one herbarium needs to be published as a second-step lectotypification. For *A. whitei* this second-step typification was undertaken by Bean (2010), for *A. petriei* and *A. philippinensis* it is published below.

Braid (1925a: 129) acknowledged Queensland Government Botanist C.T. White, who sent to Kew over "40 specimens of *Alphitonia* from Australia and New Guinea" collected by a variety of people. White seems to have numbered these specimens consecutively. The number listed for these specimens by Braid in the protologues is therefore not a collection number, but was added by White later (see also Bean 2010). These numbers are here indicated in square brackets and can be found on the K specimens and also on the duplicates retained by White in BRI.

Revision of the genus Alphitonia.—In *K.B.* 1925, p. 177, l. 8, delete the words from "or where" to "type specimens." Delete the asterisks on p. 178, l. 34 after *Ladbrook* 46; p. 181, l. 28 after *Bailey* 24; p. 184, l. 11 after *Elmer* 10335.

Fig. 2. The *addendum* to K.W. Braid's *Revision of the genus Alphitonia* (Braid 1925b).

Nomenclature

Alphitonia excelsa (A.Cunn ex Fenzl) Reissek ex Benth.

Fl. Austral. 1: 414 (1863). — *Colubrina excelsa* A.Cunn. ex Fenzl in Endl. *et al.*, *Enum. Pl.* 20 (1837). — *Ceanothus excelsus* (A.Cunn. ex Fenzl) A.Cunn ex Steud., *Nomencl. Bot. ed. 2*, 2: 313 (1841). — *Ceanothus excelsus* A.Cunn. ex Fenzl in Endl. *et al.*, *Enum. Pl.* 20 (1837), *nom. inval. pro syn.* — **Lectotype:** Moreton Bay, N.S. Wales [now Qld], 1824, *A. Cunningham s.n.* (W0059884, photo seen), *fide* A.R.Bean, *Muelleria* 28: 5 (2010). **Possible isolectotype:** BRI-AQ0317604.

Alphitonia excelsa var. *acutifolia* Braid, *Bull. Misc. Inform. Kew* 1925: 177–178 (1925). — **Type citation:** "Ipswich, *Hall* 9*". **Lectotype (here designated):** Ipswich, *T.F. Hall s.n.* [9] (K000074522, photo seen; determined by K.W. Braid). **Isolectotype:** BRI-AQ0317588 (photo seen).

Alphitonia sp. (=RFK/25763) B.P.M.Hyland & T.P.Whiffin, *Austral. Trop. Rain Forest Trees: Interactive Ident. Syst.* 1: 109, 129, 140, Code 901 (1993)

Alphitonia sp. (Forty Mile Scrub BH 25763RFK) B.P.M.Hyland, B.Gray & R.W.Elick in W.E.Cooper & W.T.Cooper, *Fr. Rainforest* 310 (1994) [Appendix I: Provisional Species List].

Alphitonia sp. (Selwyn Ranges *L.P. Conroy 3*) E.M.Ross in R.J.F.Hend. (ed.), *Queensl. Vasc. Pl. Names Distrib.* 291 (1994).

Alphitonia sp. (Little Crystal Creek *A.R. Bean 5237*) E.M.Ross in R.J.F.Hend. (ed.), *Queensl. Vasc. Pl. Names Distrib.* 291 (1994).

Alphitonia sp. (Broad-leaved Form) W.E.Cooper & W.T.Cooper, *Fr. Austral. Trop. Rainforest* 423 (2004).

Alphitonia sp. (Little Crystal Creek) W.E.Cooper & W.T.Cooper, *Fr. Austral. Trop. Rainforest* 423 (2004).

Alphitonia philippinensis auct. non Braid: C.T.White, *Proc. Roy. Soc. Queensland* 50: 66–87 (1939).

Braid (1925a) published *A. excelsa* var. *acutifolia* from specimens of the taxon provided by C.T. White. The specimen seen and annotated by Braid in preparing his description of var. *acutifolia* is designated as the lectotype, above.

As Bean (2010) mentioned, a number of phrase names have been used for local variations of the polymorphic species *A. excelsa*. Several more names that were added to the *Australian Plant Census* (APC 2020) recently, are listed here, as well.

Alphitonia franguloides A.Gray

U.S. Expl. Exped., Phan. 15: 280, pl. 22B (1854). — *Alphitonia excelsa* var. *franguloides* (A.Gray) F.M.Bailey, *Compr. Cat. Queensland Pl.* 837 (1913). — **Type citation:** "Sandalwood Bay, &c., Vanua-levu, Feejee Islands". **Lectotype:** [Mbua Bay, Vanua Levu, Fiji,] U.S. Exploring Expedition, [1840,] *C. Wilkes* (US00094511, old accession number 17196, photo seen), *fide* A.C.Sm., *Fl. Vit. Nova* 3: 695 (1985), as "holotype". **Isolectotypes:**

Fig. 3. Three Australian members of the *Alphitonia* Group. **A–F** *Alphitonia petriei*: **A** branch ×0.3; **B** flower (side view) ×7.5; **C** flower from above ×7.5; **D** stamen ×15, with characteristic appendage at the base of the anther; **E** fruit ×1.25; **F** receptacle with seeds attached ×2.5. **G–J** *A. whitei*: **G** branch ×0.3; **H** flower (side view) ×7.5; **I** flower from above ×7.5; **J** fruit ×2.5. **K–P** *Emmenosperma cunninghamii*: **K** branch ×0.3; **L** flower (side view) ×7.5; **M** flower from above ×7.5; **N** closed fruit ×2; **O** open fruit ×2; **P** seed remaining on receptacle ×2. — A *A.R. Bean 5043* (MEL721022), B–D *K.R. Thiele 2501* (CANB467468), E *F. Mueller s.n.* (MEL712882), F *I.R. Telford 11194* (CBG9102405), K–M *J. Russel-Smith 8403* (MEL1601336), N *B. Gray 1480* (MEL1605347), O, P *C.R. Dunlop 7242* (MEL1583577), G–I *A.R. Bean 5078* (MEL721328), J *V.K. Moriarty 2039* (CANB296521).

Feejee Islands, U.S. Exploring Expedition, *C. Wilkes* (K000729218, ex Herb. Benth.; NY00406510; photos seen). Feejee Islands, U.S. South Pacific Exploring Expedition 1838–42, *C. Wilkes* (GH00051228, ex US, right hand specimen; P00641644, ex US, right hand specimen; photos seen).

Smith (1985: 695) stated that the "type is U. S. Expl. Exped. (US 17196 HOLOTYPE; ISOTYPE at K)". This can be interpreted as an inadvertent lectotypification (Art. 9.10; Turland *et al.* 2018) with the term "holotype" to be corrected to "lectotype". The type specimen contains a flowering and a fruiting branch of the species. Duplicates of the expedition's specimens can be found in several herbaria.

Alphitonia franguloides is known from higher elevations and drier habitats in Fiji (Thomson & Thaman 2008). The name was applied in error to *A. whitei* by Bailey (1913), who also reduced the taxon to a variety of *A. excelsa*.

Gray (1854) also published *A. franguloides* var. *obtusa*[1] from specimens collected in Tonga during the same expedition, and this name most likely refers to *A. zizyphoides* (Sol. ex Spreng.) A.Gray, the only species of the genus recorded for Tonga (Yuncker 1959; Ellison 1990). However, other authors have synonymised this variety also with either *A. franguloides* (Hauenschild *et al.* 2018b) or *A. vieillardii* Lenorm. ex Braid (Braid 1925a).

Alphitonia petriei Braid & C.T.White

in Braid, *Bull. Misc. Inform. Kew* 1925: 178 (1925). — **Type citation:** "Johnston River, *Ladbrook* 46*; Kuranda, *White* (1525) 43*". **First-step lectotype:** Kuranda, 1 Mar. 1922, *C.T. White (1525)* [43], *fide* Braid, *Bull. Misc. Inform. Kew* 1925: 320 (1925). **Second-step lectotype (here designated):** K, specimen with loan stamp "H/1641/93 8". **Residual syntype:** Johnstone River, Oct. 1917, *H.G. Ladbrook s.n.* [46] (K, with loan stamp "H/1641/93 9"; BRI-AQ317594, photo seen).

As stated above, Braid (1925b) selected the lectotype gathering from the two specimens he had initially indicated as syntypes with an asterisk (Braid 1925a). There is no duplicate of *C.T. White* [43] specimen in BRI (Bean 2010), however, in case there are duplicates elsewhere the K specimen is here selected as lectotype. Bean (2010) designated a specimen of *Ladbrook s.n.* as lectotype in error, as he was unaware of the *addendum* by Braid (1925b), whose selection has priority.

Alphitonia philippinensis Braid

Bull. Misc. Inform. Kew 1925: 183 (1925). — **Type citation:** "Malay Archipelago. Philippines: [...] Dumaquate, *Elmer* 9432* and 10335*". **First-step lectotype:** Philippines, Island of Negros: Province of Negros Oriental, Dumaguete, Cuernos Mts., Mar. 1908, *A.D.E. Elmer 9432*, *fide* Braid, *Bull. Misc. Inform. Kew* 1925: 320 (1925). **Second-step lectotype (here designated):** K, specimen with loan stamp "H/1641/93 2". **Isolectotype:** L0383140, photo seen; NSW281006. **Residual syntype:** Philippines, Island of Negros: Province of Negros Oriental, Dumaguete, Cuernos Mts., June 1908, *A.D.E. Elmer 10335* (K, with loan stamp "H/1641/93 3"; L0383139, photo seen; NSW503021).

Bean (2010) stated that Australian material determined by C.T. White as *A. philippinensis* was in fact *A. excelsa* (White 1939) and that the name *A. philippinensis* had been later misapplied to specimens of *A. oblata* by Hyland *et al.* (2002) and Kellermann & Thiele (2008). The species is native to Malaysia, Indonesia, the Philippines, and possibly adjacent regions of Indo-China and Papua New Guinea, but more research is needed to determine the exact area of distribution.

Alphitonia pomaderroides (Fenzl) A.R.Bean

Austrobaileya 7: 377 (2006). — *Ziziphus pomaderroides* Fenzl in Endl. *et al.*, *Enum. Pl.* 20 (1837), as "*Zizyphus*". — **Type citation:** "*Cap van Diemen.* (Ferd. Bauer.)". **Holotype:** Cape Van Diemen [Mornington Is.], Dec. 1802, *F. Bauer* (W0002221, photo seen).

Alphitonia obtusifolia R.Br. ex Braid, *Bull. Misc. Inform. Kew* 1925: 182 (1925). — **Type citation:** "Queensland and Region of Gulf of Carpentaria. Carpentaria, *Brown* 5364,*". **Lectotype (here designated):** Carpentaria Island C, [i.e. Allen Island, Gulf of Carpentaria, Qld, 20 Nov.] 1802, *R. Brown Iter Austral. 5364* (BM000839293). **Isolectotype:** Carpentaria, *R. Brown Iter Austral. 5364* (K, with loan stamp "H/1641/93 6", determined by K.W. Braid, labelled as "Holotype" by K.R. Thiele & J.G. West). **Possible isolectotypes:** North Coast (BRI-AQ0317590, photo seen; CANB278602; E00769942, photo seen; NSW281104).

Alphitonia obtusifolia var. *tenuis* Braid, *Bull. Misc. Inform. Kew* 1925: 183 (1925). — **Type citation:** ""North Coast," *R. Brown**". **Lectotype (here designated):** North Coast, [Qld, Nov. 1802,] *R. Brown s.n.* (K; with loan stamp "H/1641/93 5", determined by K.W. Braid). **Possible isolectotype:** North Coast (P06791109, photo seen).

["*Ceanothoides obtusifolia*" R.Br. *in sched.*, *fide* Braid, *Bull. Misc. Inform. Kew* 1925: 182 (1925), *et* A.R.Bean, *Muelleria* 28: 8 (2010) (both as "*Caenothoides*"), *nom. inval. pro syn.*]

Only one specimen of Ferdinand Bauer's collection of *Ziziphus pomaderroides* is known from the Herbarium in Vienna, where Fenzl worked at the time (Fenzl

1 *Alphitonia franguloides* var. ? β *obtusa* A.Gray, *U.S. Expl. Exped., Phan.* 15: 278 (1854). — **Type citation:** "Tongatabu : in fruit only". **Syntypes:** Tongatabu, U.S. Exploring Expedition, *C. Wilkes* (US00094512, old accession number 17197, photo seen); Tonga or Friendly Islands, U.S. South Pacific Exploring Expedition 1838–42, *C. Wilkes* (GH00051228, ex US, left hand specimen, photo seen); [wrongly labelled as "Feejee Islands",] U.S. South Pacific Exploring Expedition 1838–42, *C. Wilkes* (P00641644, ex US, left hand specimen, photo seen).

1837); this is accepted here as holotype of the species, as indicated by Bean (2006).

The synonym *A. obtusifolia* was described by Braid from a Robert Brown "specimen [...] in the British Museum, and a duplicate specimen [...] in the Kew Herbarium" (Braid 1925a: 182), indicating that he considers the main type specimen to be at BM. This is in contrast to Bean (2010), who stated in his revision of the genus for Australia that the holotype could be found in K (the same information is repeated by Hauenschild *et al.* 2018b).

While today only one sheet of *R. Brown Iter Austral. 5364* is at BM, in Braid's time, however, more material of the species was available in London and most likely seen by him during the preparation of his revision. Duplicates of Brown's specimens have been distributed by BM to many institutions since the 1970s, including a large number sent to Australian herbaria[2]. Hence it cannot be assumed that the single specimen currently in BM is the holotype of the name (see McNeill 2014). To clarify the situation, the specimen at BM is here designated as the lectotype. The K isolectotype carries the same Bennett Number as the lectotype and was also determined by Braid.

The location details of Brown duplicates are very sparse. Two duplicates from CANB and NSW bear Brown's original label "North Coast", but were distributed by BM with an additional label stating the location as "Allen Island". The BRI duplicate has a label "North Coast", possibly written by J.J. Bennett, who catalogued Brown's collections, and a second label by S.T. Blake, stating that he had determined the location as Allen Island from Brown's manuscripts. A specimen at E is similarly labelled. None of these specimens bear the Bennett Number *5364* and are accepted here as possible isolectotypes of *A. obtusifolia* and not original material of var. *tenuis*.

Only one Brown specimen at K bears Braid's determination *A. obtusifolia* var. *tenuis*. However, as there are multiple other specimens with the location "North Coast" (see above), this is here designated as the lectotype of that name. A specimen at P is possibly an isolectotype, it has been determined as var. *tenuis* by Jacques Florence.

Braid (1925a) and Bean (2010) mention Robert Brown's manuscript name, and both misspelt it as "*Caenothoides obtusifolia*". However, the lectotype is labelled by Brown as "*Ceanothoides obtusifolia*", i.e. he compared it with the well-known Californian genus *Ceanothus* L. Burbidge (1955) stated that a "large number of names employed by Brown are what he called himself [...] "nicknames"", with the suffix *-oides* indicating an affinity to an existing genus. Almost all Brown collections mentioned above were labelled by him with this name.

Brown generally used "*Ceanothoides*" as a nickname on specimens of Rhamnaceae that he regarded to belong to new genera. It can be found on the original labels of many specimens that are now in *Alphitonia* Endl., *Colubrina* Rich. ex Brongn., *Discaria* Hook., *Pomaderris* Labill., *Trymalium* Fenzl and *Spyridium* Fenzl. (unpubl. data).

Alphitonia whitei Braid

Bull. Misc. Inform. Kew 1925: 181 (1925). — **Type citation:** "Near Barron River, *Bailey* (24)* [...] Jordan Creek, *Mocatta* 23*". **First-step lectotype:** Jordan Creek, Innisfail district, Nov. 1912, *H.W. Mocatta s.n.* [23], *fide* Braid, *Bull. Misc. Inform. Kew* 1925: 320 (1925). **Second-step lectotype:** K000074521, *fide* A.R.Bean, *Muelleria* 28: 10 (2010). **Isolectotype:** BRI-AQ0317596. **Residual syntype:** Boar Pocket nr. Barron River, 25 June 1899, *J.F. Bailey* [24] (K000729496; BRI-AQ0317598).

Alphitonia franguloides auct. non A.Gray: F.M.Bailey, *Compr. Cat. Queensland Pl.* 837 (1913).

Alphitonia excelsa var. *franguloides auct. non* (A.Gray) F.M.Bailey: F.M.Bailey, *Compr. Cat. Queensland Pl.* 837 (1913).

Following the method described above, the lectotype of this name was chosen in a two-step process: Braid (1925b) selected the gathering, *Mocatta s.n.* [23], by deleting the asterisk from the Bailey specimen mentioned in the protologue, and Bean (2010) chose the specimen at K as the second-step lectotype.

Emmenosperma cunninghamii Benth.

Fl. Austral. 1: 415 (1863), as "*Emmenospermum* (?)". — **Type citation:** "Port Warrender, N.W. coast, A. Cunningham. The specimens are very imperfect; they were referred to *Croton* by Cunningham". **Lectotype (here designated):** "Croton miltospermum A.Cunn. / Port Warrender / N.W. Australia", Oct. 1819, *A. Cunningham 476* (K0007299222, presented by R. Heward, 1862, photo seen). **Isolectotypes:** "Port Warrender N.W. Coast / 2nd Voyage of Mermaid" 1819, *A. Cunningham 476* (BM000838394, photo seen). "Croton miltospermum / C / Port Warrender", *A. Cunningham s.n.* (K000729221, photo seen).

There are three Cunningham specimens of the taxon present at K and BM, all in the fruiting stage. Two of the three specimens (BM000838394, K0007299222) have fruits and seeds present; in the third specimen (K000729221), all seeds have been shed, i.e. it is now sterile. The specimen with seeds that is annotated with Cunningham's manuscript name "*Croton miltospermum*", mentioned in the protologue by

2 For example, 123 specimens collected by Robert Brown and Allan Cunningham were sent by BM to the Forest Research Institute, Canberra (FRI), in 1974 (Chippendale 1976) and are now incorporated into CANB; in 1978 CANB received 1069 specimens (Eichler 1978) and NSW "a large number of duplicates" (Briggs 1979); around the year 2000 some duplicates were sent to HO (Tasmanian Herbarium 2003).

Bentham (1863), is chosen as the lectotype. While Bentham published the species with a question mark, this is possibly related to its generic placement, but the taxon was nonetheless accepted by him (Art. 36.1; Turland *et al.* 2018).

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A key to the species of *Swainsona* (Fabaceae) in Western Australia and description of *S. katjarra* from the Little Sandy Desert region, Western Australia

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Abstract: A new dichotomous identification key is presented for all 48 species and two phrase-names of *Swainsona* in Western Australia. Important distinguishing characters used throughout the key are discussed. A new entity from the Little Sandy Desert, Western Australia, was recognised during the course of work on this key and is described here as the new species *Swainsona katjarra* R.W.Davis & T.Hammer.

Keywords: Fabaceae, Faboideae, identification key, new species, *Swainsona*, taxonomy, Western Australia

Introduction

The endemic Australian genus *Swainsona* Salisb. (Fabaceae: Faboideae) comprises c. 95 species, of which 47 are native to Western Australia. There has only been one new species described in Western Australia in the over 26 years since the revision of the genus by Thompson (1993), namely *S. thompsoniana* R.W.Davis & P.J.H.Hurter (Davis & Hurter 2013). Thompson's revision included a key to the 85 known species of the genus and its early steps were based on indumentum characters, including hair type, length, thickness and orientation. At times, these hair characters are difficult to interpret and are subject to infraspecific variation. These ambiguities within the key have made it difficult to distinguish between taxa.

The current paper presents a dichotomous key to *Swainsona* in Western Australia, elucidating ambiguities by utilising floral morphological characters that are easier to distinguish. The construction of this key led to the discovery of a new species from the Little Sandy Desert region, Western Australia, described here as *Swainsona katjarra* R.W.Davis & T.Hammer. In total, 48 species and two phrase name taxa are present in the State. An electronic version of the key on KeyBase is available through the Flowering Plants of Western Australia project (https://keybase.rbg.vic.gov.au/), and a Lucid key version will be made available on FloraBase (https://florabase.dpaw.wa.gov.au/).

Methods

This study was based on examination of dried specimens of *Swainsona* housed at PERTH. Specimens were critically evaluated irrespective of current determinations and compared to the protologues and type specimens. All species names follow the taxonomy on FloraBase, and proper author citations can be found there. We have excluded *Swainsona* sp. Shark Bay (*M.E. Trudgen 7588*) from this key, as our observations suggest it is conspecific with *Swainsona longicarinata* Joy Thomps. and this will be treated in a forthcoming paper.

Distinguishing characters

Thompson (1993) discusses the difficulties and variability of floral and vegetative characters in *Swainsona*. These are often compounded by the lack of adequate material, the remoteness of many species and variability due to different seasonal conditions. Herbarium vouchers often lack mature fruiting specimens. Also, the lack of field observations and availability of fresh material have been a hinderance to taxonomic resolution. The following sections are clarifications of the distinguishing characters based on our assessment, which are to facilitate the use of the key.

Indumentum. Indumentum types can be difficult to interpret as hair types can vary on different parts of the plant. We have simplified hair type into three groups. Some species have long fine basifixed hairs tapering

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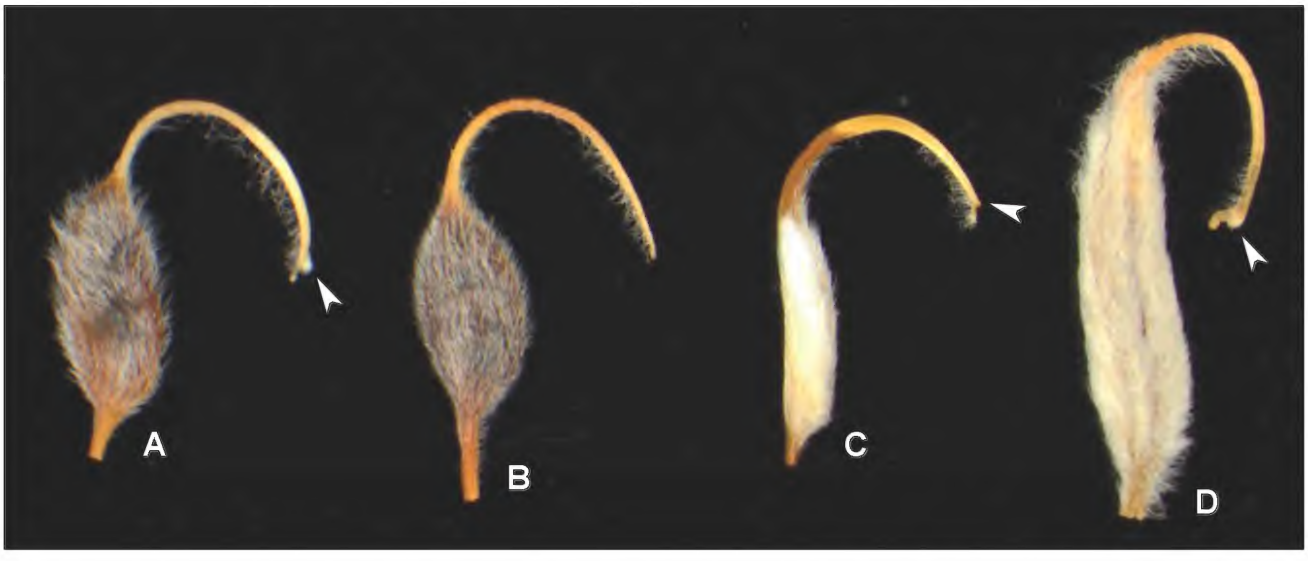

Fig. 1. Representative style characters: **A** style with abaxial tuft of hairs (arrow) (*Swainsona decurrens*); **B** style without abaxial tuft of hairs (*S. forresti*); **C** geniculate style tip (arrow), style without abaxial tuft of hairs (*S. tenuis*); **D** geniculate style tip, style with abaxial tuft of hairs (arrow) (*S. unifoliata*). — A *A.A. Mitchell PRP 442* (PERTH04580222), B *J.S. Beard 6054* (PERTH03258955), C *A.S. George 11986* (PERTH03257584), D *C.A. Gardner 14521* (PERTH06205917).

towards a fine tip; these may be either spreading to ascending. Other species have short, broad, turgid hairs; these are appressed and rarely more than 0.3 mm long. A few species have medifixed hairs; these are usually appressed and at times may be difficult to distinguish but can often be recognised because both ends of the hairs have a sharply tapering point.

Vegetative characters. Stipule lobe characters are used where consistent within species; as stipule shape and lobing can vary on a single individual. The presence or absence of a pulvinus at the base of the inflorescences is used in the recognition of species; it may be wrinkled or expanded and lightly or darkly coloured. We have used this character sparingly, and only when it is clear and consistent. Bract and bracteoles are variable in shape, size and indumentum and may be diagnostic; we have used bract length in relation to pedicel length rather than absolute size for convenience.

Perianth. Calyx lobe length can be variable and in some cases the length of calyx tube relative to lobe length is a useful distinguishing feature. The standard in most species is uniformly textured, but some species have distinctly thickened tissue where the standard meets the claw, either in the form of two parallel ribs running down the centre of the standard or two prominent thickened pads. Wing and keel shapes are useful in species recognition. The presence, orientation and shape of the auricle is helpful, as is the width of the sinus, and the distance between the auricle and claw of the wing and keel. The presence of pockets and folds in the keel, usually found below the auricle, may be useful in the field, however, the shape and form of these is difficult to ascertain in dried material and have not been used in the key. We use the presence or absence of a keel apex appendage at the start of the key. Three species have an appendage at the apex of the keel: one (*Swainsona cornuta*) bears a long attenuate appendage the keel tip, while two have a subtle boss-like or knob-shaped keel apex. In all remaining species the keel apex is entire, evenly acute to obtuse, and without appendages.

Gynoecium. The style shape and position of stylar hairs are strongly diagnostic (Fig. 1). The style is evenly curved in all species but to varying degrees and either with, or without, an elbow or geniculate bend at the tip (Fig. 1C, D). While all species have a long row of hairs on the adaxial section of the style, some have an additional tuft of hairs on the abaxial portion of the style tip (Fig. 1B, D). Style hairs on *Swainsona* facilitate pollen presentation: the developing style pushes through the anthers, distributing pollen on the hairs on the adaxial surface resulting in a long continuous wall of pollen on the inner portion of the style at anthesis. Species that have a tuft of hairs on the abaxial surface of the style tip also gain a prominent cluster of pollen at the style tip.

Taxonomy

Swainsona katjarra R.W.Davis & T.Hammer, *sp. nov.*

Holotypus: S side of Carnarvon Range, Birriliburu Indigenous Protected Area, 12 Aug. 2012, *N. Gibson, S. van Leeuwen, M.A. Langley & K. Brown NG 6731* (PERTH08972311). **Isotypus:** AD [to be distributed].

An open *annual herb* to 50 cm high, with several stems radiating from a slender taproot. *Stems* 2.5–5 mm wide, slightly compressed, with fine, slender, spreading to ascending, basifixed hairs to 1 mm long. *Leaves* 60–90 mm long, with 4–6 leaflet pairs and a terminal leaflet above an extended petiolule, 15–20 mm long; leaflets obovate to elliptical, 10–20 mm long, 4–8 mm wide;

adaxial surface mostly glabrous except for sparse, long, fine, spreading hairs towards leaflet margins; abaxial surface with a sparse even covering of long, fine, hairs. *Stipules* narrow to broadly triangular, 8–10 mm long, 1–4 mm wide, margins entire or with 2–3 toothed lobes; both surfaces evenly covered with long, fine, spreading hairs. *Racemes* 10–20 cm long, 15–25 flowered. *Peduncle* slender, terete, 5–7 cm wide, with sparse spreading to ascending hairs to 1 mm long; pulvinus absent. *Bracts* narrowly triangular, 2–3 mm long, outer surface with long fine spreading hairs to 1 mm long, inner surface glabrous. *Flowers* magenta, 8–11 mm long; pedicles shorter than bracts, 2–2.5 mm long, with even cover of fine, ascending hairs to 0.5 mm long. *Calyx* tube 2–3 mm long, slightly expanding towards the top, with even covering of spreading to ascending hairs to 0.8 mm long; bracteoles narrowly triangular, 0.8–1.2 mm long, with sparse, fine hairs; calyx lobes narrowly triangular, 3.5–4.5 mm long, with a covering of sparse, fine hairs to 1 mm long. *Standard* magenta, eyes at the base of standard white, 12–12.5 mm long, 11–12 mm wide; claw shortly tapering, 3–4 mm long. *Wing* oblong, constricted in the middle and slightly upwardly curved, purple, 9.5–11 mm long, 3.5–4.5 mm deep; upper portion of wing with white curved marking. *Keel* purple, 11–12 mm long, 5.5–5.8 mm deep. *Ovary* elliptic, 3.8–4.1 mm long, with a dense covering of fine, appressed to ascending hairs to 0.5 mm long. *Ovules* numerous. *Style* geniculate, flattened, short, stout, and strongly upwardly curved, 4.5–5 mm long, with hairs along the adaxial edge and in an abaxial tuft. *Fruit* (immature) elliptical, straight, laterally compressed, 8–10 mm long, with even covering of long fine, spreading to ascending hairs to 1 mm long. **Fig. 2.**

Diagnostic features. The new species can be distinguished from all other species in genus by the following combination of characters: bracteoles minute and shorter than calyx tube, calyx lobes clearly longer than the calyx tube, upper wing surface with a hemispherical white mark, keel without appendages on the apex, style geniculate with a tuft of hairs on its abaxial surface, and fruit straight, unornamented and with fine spreading hairs.

Phenology. Both known specimens were collected in August in flower and early fruit.

Distribution and habitat. The species is known only from the Carnarvon Range (*Katjarra*) in the Little Sandy

Fig. 2. *Swainsona katjarra*: **A** habit *in situ* (type location); **B** inflorescence. — *N. Gibson, S. van Leeuwen, M.A. Langley & K. Brown NG 6731* (PERTH). Photos: K. Brown.

Desert IBRA region, Western Australia (Department of the Environment 2018). The habitat is described as *Eucalyptus camaldulensis* open woodland over mulga, *Melaleuca* sp. and *Grevillea spinosa* shrubland.

Conservation status. The species has yet to be listed by Smith & Jones (2020) under the Conservation Codes for Western Australian Flora. Only two populations, approximately 600 m apart, have been recorded to date and numbers in these populations are unknown. The conservation status of this taxon should be urgently assessed.

Proposed Vernacular Name. Birriliburu swainsona.

Etymology. The epithet *Katjarra* is the Birriliburu (southern Martu) word for the Carnarvon Range, where the only known populations occur.

Notes. Measurements were taken from slightly immature fruit for this description and the mature fruit may be longer.

Other specimens examined

WESTERN AUSTRALIA. S side of Carnavon Range, Birriliburu Indigenous Protected Area, 12 Aug. 2012, *N. Gibson, S. van Leeuwen, M.A. Langley, K. Brown NG 6730* (PERTH08972303).

Key to the species of *Swainsona* in Western Australia

Taxa marked with an asterisk appear more than once in the key.

1. Keel with two awn-like or boss-like appendages on or near the keel apex
- **2.** Keel appendage boss-like or rounded
  - **3.** Style apex with abaxial tuft of hairs . . . . . *S. incei*
  - **3:** Style apex without abaxial tuft of hairs . . . . . *S. canescens*
- **2:** Keel appendage awn-like or attenuate . . . . . *S. cornuta*

1: Keel without appendages on apex
- **4.** Style geniculate
  - **5.** Abaxial tuft of hairs present behind the style tip or rarely with a row of sparse hairs
    - **6.** Bracteoles longer than or equal to calyx tube
      - **7.** Calyx lobes narrow; keel greenish-yellow . . . . . *S. flavicarinata*
      - **7:** Calyx lobes broad; keel not greenish-yellow . . . . . *S. disjuncta*
    - **6:** Bracteoles minute, shorter than calyx tube
      - **8.** Hypanthium with sparse appressed turgid hairs; fruit tightly curved with ornamented surface and appressed turgid hairs
        - **9.** Leaflets 1–7, 10–50 mm long . . . . . *S. cyclocarpa*
        - **9:** Leaflets 9–13, 1–7 mm long . . . . . *S. halophila*
      - **8:** Hypanthium with fine spreading hairs; fruit straight, not ornamented with turgid hairs
        - **10.** Calyx lobes clearly longer than the calyx tube; upper wing surface with curved white marking . . . . . ***S. katjarra***
        - **10:** Calyx lobes clearly shorter than the calyx tube; upper wing surface without markings
          - **11.** Leaves broadly obovate to ovate, unifoliolate leaves common; fruit much longer than wide . . . . . *S. unifoliolata*
          - **11:** Leaves narrowly lanceolate to elliptical, rarely with unifoliolate leaves; fruit only slightly longer than wide. . . . . *S. oroboides**
  - **5:** Abaxial tuft or row of hairs absent behind style tip
    - **12.** Adaxial hairs in a single row on distal portion of style; fruit with scattered hairs
      - **13.** Standard with two vertical thickenings sometimes merged at the claw
        - **14.** Sinus of the wing broad and rounded . . . . . *S. paucifoliolata*
        - **14:** Sinus of the wing narrowly tapering . . . . . *S. tenuis*
      - **13:** Standard with hardened tissue at the apex of the claw, without two vertical thickenings
        - **15.** Standard apex with a mucronate tip . . . . . *S. campestris*
        - **15:** Standard apex without a mucronate tip . . . . . *S. oroboides**
    - **12:** Adaxial hairs in two distinct rows on distal portion of style; fruit glabrous except for row of hairs at the base of the suture . . . . . *S. pterostylis*
- **4:** Style not geniculate
  - **16.** Tuft of hairs present on abaxial surface of style
    - **17.** Ovary and fruit variously hairy

18. Leaves and stems with ascending or appressed turgid hairs
19. Leaves and stems without medifixed hairs
20. Bracts narrowly lanceolate to ovate; bracteoles attenuate
21. Erect annual herb; flowers mauve to maroon; fruit 10–13 mm long . . . . . *S. complanata**
21: Prostrate annual or perennial herb; flowers cream-green or sometimes tinged pink; fruit 10–25 mm long . . . . . .*S. oliveri*
20: Bracts broadly ovate; bracteoles ovate
22. Stipules strongly toothed; standard > 8 mm wide, with thickenings at the base . . . . . *S. laciniata*
22: Stipules sparsely lobed; standard < 8 mm wide, without thickenings at the base . . . *S. paradoxa*
19: Leaves and stems with medifixed hairs
23. Flowers 1–4 per raceme, without pulvinus at base of peduncle . . . . . *S. rotunda*
23: More than 5 flowers per raceme, with pulvinus at base of peduncle . . . . . .*S. microcalyx*
18: Leaves and stems with spreading or ascending fine hairs
24. Inflorescences with > 4 flowers
25. Flowers < 10 mm long
26. Calyx lobe broad-triangular, clearly shorter than calyx tube. . . . . *S. complanata**
26: Calyx lobe narrow-triangular, equal to or longer than calyx tube
27. Keel auricle recurved. . . . . .*S. decurrens**
27: Keel auricle broad-erect. . . . . *S. villosa*
25: Flowers > 15 mm long . . . . . *S. ecallosa*
24: Inflorescences with 1–3 flowers . . . . . *S. leeana*
17: Ovary and fruit glabrous
28. Leaves and stems variously hairy; fruit < 10 mm long
29. Stems and leaves with dense (sometimes sparse) turgid hairs
30. Leaves usually with 7–25 leaflets; style tip narrowing from the top with narrowed piece variously extended . . . . . .*S. affinis*
30: Leaves usually with 21–41 leaflets; style tip usually truncate . . . . . *S. microphylla*
29: Stems and leaves usually with dense (sometimes sparse) long, fine spreading hairs . . . .*S. decurrens**
28: Leaves and stems glabrous; fruit ≥ 10 mm long
31. Stipules broadly elliptical; fruit 30–40 mm long . . . . . *S. colutoides*
31: Stipules narrowly lanceolate; fruit 10–12 mm long . . . . . *S. stenodonta**
16: Tuft of hairs absent on abaxial surface of style
32. Keel > 25 mm long
33. Keel long and tapering to a point; sprawling annual or short-lived perennial . . . . . *S. formosa*
33: Keel rounded; erect annual to 2 m . . . . . *S. maccullochiana*
32: Keel < 25 mm long
34. Stipule lobes present
35. Pulvinus absent at base of peduncle
36. Hypanthium with long spreading hairs; calyx lobes ± twice as long as tube . . . . . .*S. tanamiensis*
36: Hypanthium with short appressed turgid hairs; calyx lobes shorter than or equal to tube. . . . . .*S. elegantoides**
35: Pulvinus present at base of peduncle
37. Hypanthium with long fine spreading hairs
38. Keel < 12 mm long
39. Keel to 9 mm long; auricle barely visible
40. Calyx lobes twice the length of tube; fruit with long pilose hairs, >1 mm long . . . . . *S. longipilosa*
40: Calyx lobes shorter than tube; fruit with short hairs, < 0.4 mm long . . . . . *S.* sp. Burnerbinmah (*D. Edinger et al. 38*)
39: Keel greater than 10 mm long; auricle clearly visible
41. Keel conspicuously longer than the wings; lamina on wing auricle glabrous . . . *S. calcicola*
41: Keel scarcely longer than the wings; lamina on wing auricle hairy . . . . . .*S. elegans*
38: Keel > 15 mm long. . . . . *S. beasleyana*
37: Hypanthium with turgid appressed hairs. . . . . *S. gracilis*

34: Stipule lobes absent
42. Calyx tube glabrous (or rarely with the odd hair)
43. Pulvinus absent at base of peduncle
44. Stipules attenuate not leaf-like, < 5 mm long
45. Wings straight, much shorter than keel
46. Stems erect, glabrous or with fine hairs; flowers dark red . . . . . *S. stenodonta**
46: Stems prostrate, glabrous or with a mixture of fine and turgid hairs; flowers mauve with yellow centres . . . . . *S. thompsoniana*
45: Wing crescent-shaped, much longer than keel . . . . . *S. campylantha*
44: Stipules ovate, leaf-like, 6–20 mm long . . . . . *S. kingii*
43: Pulvinus present at base of peduncle . . . . . *S. pedunculata*
42: Calyx tube conspicuously hairy
47. Style apex broadly flattened spoon-like, with two rows of hairs . . . . . *S. rostellata*
47: Style apex tapering, not flattening, with single row of hairs
48. Pulvinus present at base of peduncle
49. Two conspicuous horizontal flaps at the base of the standard present . . . . . *S. longicarinata*
49: Two conspicuous horizontal flaps at the base of the standard absent
50. Wing conspicuously shorter than keel. . . . . *S. phacoides*
50: Wing equal to or longer than keel . . . . . *S. purpurea*
48: Pulvinus absent at base of peduncle
51. Keel apex flattened and twisted. . . . . *S. acuticarinata*
51: Keel apex rounded and not twisted
52. Bracts rounded to broadly ovate, bases cordate . . . . . *S. perlonga*
52: Bracts attenuate to narrowly ovate, bases not cordate
53. Stem hairs fine spreading or upwardly curved
54. Stem hairs upwardly curved, to 0.5 mm long. . . . . *S. forrestii*
54: Stem hairs spreading, to 2 mm long . . . . . *S. elegantoides**
53: Stem hairs turgid and appressed . . . . . S. sp. Brooking Gorge (*A. Markey & K. Brown FV 11506*)

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A review of Colletieae and *Discaria* (Rhamnaceae) in Australia

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Abstract: The tribe Colletieae (Rhamnaceae) is reviewed for Australia. It is primarily South American, but two species of *Discaria* Hook., *D. pubescens* (Brongn.) Druce and *D. nitida* Tortosa, occur in south-eastern Australia and Tasmania. The two species are described and illustrated. A hybrid taxon sometimes occurs in areas where the two species are sympatric. The history and typification of the name *D. pubescens* and its synonyms is discussed and clarified.

Keywords: Taxonomy, nomenclature, pre-1958 holotype, Rhamnaceae, Colletieae, *Discaria*, South America, Australia, New South Wales, Queensland, Tasmania, Victoria

Introduction

The tribe Colletieae Reiss. ex Endl. is comprised of 23 species in seven genera: *Adolphia* Meisn., *Colletia* Comm. ex A.Juss., *Discaria* Hook., *Kentrothamnus* Suess. & Overkott, *Ochetophila* Poepp. ex Endl., *Retanilla* (DC.) Brongn. and *Trevoa* Miers ex Hook. The maximal species diversity of the tribe is found south of 30° S and most of the distributions are loosely associated with the Andes in South America, but the tribe also includes a genus of Gondwanan distribution, *Discaria*, with members found in South America, Australia and New Zealand.

The circumscription of Colletieae has never been disputed. Decussate leaves, abundance of spines, and presence of serial meristems in the leaf axils have traditionally been the diagnostic characters of the tribe (e.g. Miers 1860; Suessenguth 1953; Medan & Schirarend 2004). All species of the tribe exhibit the ability to form root nodules and fix nitrogen in symbiosis with *Frankia bacteria*, a feature that is also present in the genus *Ceanothus* L. in Rhamnaceae (Medan & Tortosa 1976, 1981; Rundel & Neel 1978; Clawson *et al.* 1998; Ganguli & Kennedy 2013).

Colletieae is one of the best studied tribes in Rhamnaceae; all genera of the tribe have been revised (Johnston 1973; Tortosa 1983b, 1989, 1992, 1993; Kellermann *et al.* 2005). The morphology of its taxa is well known and reproductive biology, pollination, flower structure and ultramorphology has been studied extensively (e.g. Medan 1985, 1986; Medan & Aagesen 1995; Tortosa *et al.* 1996; Aagesen 1999 and references therein; Gotelli *et al.* 2012a, 2012b, 2020; Medan & Devoto 2017 and references therein).

Monophyly has been corroborated by a morphological analysis of the tribe (Aagesen 1999), by molecular analyses at family level (Richardson *et al.* 2000; Hauenschild *et al.* 2016, 2018), by analyses of nearly all species of the tribe combining morphology with *trn*L-F sequence data (Aagesen *et al.* 2005) and of *trn*L-F data alone (Kalwij *et al.* 2019). According to Kalwij *et al.* (2019) and Hauenschild *et al.* (2018), the Colletieae clade has a trichotomy at its base, consisting of *Kentrothamnus* and two main clades. The first clade contains *Trevoa* and *Retanilla*. The second clade combines *Adolphia*, *Discaria*, *Colletia* and *Ochetophila*. Until recently, species of *Ochetophila* were included in *Discaria* (Tortosa 1983b; Aagesen 1999), but after Aagesen *et al.* (2005) reported that this renders *Discaria* polyphyletic, the genus *Ochetophila* was reinstated by Kellermann *et al.* (2005).

Discaria is now a genus of six species, three of which are found outside South America. *Discaria pubescens* (Brongn.) Druce occurs from Queensland to Victoria and in Tasmania, mainly on the tablelands and at higher altitudes; *Discaria nitida* Tortosa is a rare species known from a few localities in New South Wales and Victoria (Curtis 1956; Walsh & Udovicic 1999; Harden 2000). *Discaria toumatou* Raoul, occurs in New Zealand, where it is most common on the South Island; it has also been recorded on the Chatham Islands (Allan 1961).

Keogh & Bannister (1993) concluded that trans-oceanic dispersal seems highly improbable in the genus, which suggests that the amphiantarctic disjunction

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of *Discaria* may be as old as the separation of South America-Antarctica from Australia-New Zealand, i.e. well over 30 million years old (Hinojosa & Vallagrán 1997; McLoughlin 2001). Richardson *et al.* (2004), however, estimate the age of the Colletieae clade to be only 14.6 ± 3.0 MYA, when analysing *rbc*L and *trn*L-F sequence data, but the results of this analysis have also been considered to be a considerable under-estimation (Ladiges *et al.* 2005). Recently, van Santen & Linder (2020) estimate the split between Pomaderreae and Colletieae to be 42.9 MYA using eight chloroplast and nuclear regions, however the confidence intervals in their phylogeny are quite large and *Adolphia* groups with the unrelated Pomaderreae, hence an estimate for the tribe Colletieae cannot be ascertained.

The ecology and distribution of the Australian species have been described for *D. pubescens* in Victoria (Willis 1955; Hall & Parsons 1987; Lunt 1987) and Tasmania (Coates 1991). Wright & Briggs (2000) examined populations of *D. nana* in N.S.W. *Discaria toumatou* has been investigated extensively regarding its breeding system (Primack & Lloyd 1980), seed morphology and dispersal mechanisms (Keogh & Bannister 1993, 1994), structure of root-nodules (Newcomb & Pankhurst 1982) and spine morphology and development (Cockayne 1905, 1922).

Discaria including *Ochetophila* has been revised by Tortosa (1983b), who only had access to a limited amount of Australian material. Since then, more collections have become available, enabling us to present an up-dated account of *Discaria* in preparation for the forthcoming *Flora of Australia* treatment of the family.

Taxonomy

Rhamnaceae trib. **Colletieae** Reissek ex Endl.

Gen. Pl. 1099 (1840). — **Type:** *Colletia* Comm. ex Juss.

Armed *shrubs* or small trees, usually with opposite-decussate cladodes and reduced leaves; actinorhizal root nodules present. *Fruit* a papery nut, fleshy drupe or (in Australia) capsular, exploding at maturity to disperse the seeds leaving a disc-like hypanthium torus.

Size & Distribution: Seven genera with 20 species, mainly distributed in extra-tropical South and Central America: *Adolphia* Meisn. (1 sp.), *Colletia* Comm. ex A.Juss. (5 spp.), *Discaria* Hook. (6 spp.), *Kentrothamnus* Suess. & Overkott (1 sp.), *Ochetophila* Poepp. ex Endl. (2 spp.), *Retanilla* (DC.) Brongn. (4 spp.) and *Trevoa* Miers ex Hook. (1 spp.).

Adolphia spreads to southern North America. *Discaria* extends to New Zealand and Australia. One species, *O. nana* (Clos) Kellermann, Medan & Aagesen, has been dispersed to subantarctic Marion Island by vagrant birds (Kalwij *et al.* 2019).

Discaria Hook.

Bot. Misc. 1: 156 (1829). — *Discaria* sect. *Pentapasma* Endl., *Gen. Pl.* 1: 1099 (1840), *nom. inval.* (= sect. *Discaria*). — *Discaria* Hook. sect. *Discaria*: Rchb., *Deut. Bot. Herb.-Buch* 144 (1841); Suess., *Mitt. Bot. Staatssamml. München* 1(8): 355 (1953). — **Type:** *Discaria americana* Gillies & Hook., *fide* Pfeiff., *Nomencl. Bot.* 1: 1108 (1874).

Tetrapasma G.Don, *Gen. Hist.* 2: 22, 40 (1832). — *Discaria* sect. *Tetrapasma* (G.Don) Reissek ex Endl., *Gen. Pl.* 1: 1099 (1840). — *Tetrasperma* Steud., *Nomencl. Bot. ed. 2*, 2: 673 (1841), *orth. var.* — *Tetraspora* Hook., *Fl. Tasman.* 1: 69 (1855), *orth var.*, *non* Link ex Desv., *Observ. Pl. Angers* 17 (1818). — **Type:** *Tetrapasma juncea* G.Don (by monotypy).

Solenantha G.Don, *Gen. Hist.* 2: 22, 39 (1832). — **Type:** *Solenantha spinosa* G.Don (by monotypy).

×*Notophaena* Miers, *Ann. Mag. Nat. Hist. ser. 3*, 5: 267 (1860). — *Discaria* sect. *Notophaena* (Miers) Suess., *Mitt. Bot. Staatssamml. München* 1(8): 355 (1953). — **Type:** *Colletia* ×*serratifolia* Vent. ≡ *Notophaena* ×*serratifolia* (Vent.) Miers ≡ *Discaria* ×*serratifolia* (Vent.) Benth. & Hook.f. ex Mast. = *Discaria chacaye* (G.Don) Tortosa × *D. articulata* (Phil.) Miers.

Evergreen or semideciduous *shrubs*, usually with spinescent short shoots. *Leaves* opposite, petiolate; stipules triangular, connate behind the petiole, persistent. *Flowers* bisexual, 4–5-merous, white or cream, in axillary clusters of up to 50 flowers. *Hypanthium* shortly tubular. *Sepals* erect to recurved, caducous. *Petals* cucullate, not clawed, incurved or erect, or absent. *Stamens* shorter than or subequal to petals, incurved or erect. *Disc* conspicuous, lining the hypanthium or forming a sinuous ring around the ovary, smooth, glabrous. *Ovary* half-inferior; carpels 3 (or 4); style entire or branched, glabrous. *Fruit* brown, a globular capsule; torus basal. Seed brown.

***Typification of* ×Notophaena.** When Miers (1860) described *Notophaena*, he included eight species and stated that "[T]he type of the genus is the *Colletia serratifolia* by Ventenat". Of these eight names, four are now synonyms of *D. chacaye* (G.Don) Tortosa, *N. tomentosa* (Phil.) Miers is a synonym of *Colletia hystrix* Clos and one is still accepted, but in *Discaria*: the new Zealand *D. toumatou*. Two other taxa have shown to be of hybrid origin (Tortosa 1983a), including the type, *C. serratifolia*. As such, this synonym of *Discaria* is listed here as a nothogenus, ×*Notophaena*.

Size & distribution. A genus of six species, mostly in extra-tropical South America, with one species in New Zealand and two in south-eastern Australia.

Notes. *Discaria* is notable for usually having two meristems in the axil of each leaf. The distal meristem usually develops into a spiny branch, whilst the proximal meristem develops into a short shoot that bears leaves and flowers (see Tortosa *et al.* 1996 for detailed discussion). Both Australian species are

Key to species of *Discaria* in Australia

1. Spines (15–) 25–70 mm long; leaves usually caducous; petals present; style entire or minutely lobed . . . . . **1. *D. pubescens***

1: Spines 5–15 (–18) mm long; leaves usually persistent; petals absent; style branched . . . . . **2. *D. nitida***

uncommon and many declining populations are threatened by agricultural clearing and grazing.

The basic chromosome number of most Colletieae, including the New Zealand *D. toumatou* is x=11 (Dawson 2000; Medan & Schirarend 2004). No chromosome counts have been published for the Australian species.

Etymology. Derived from the Greek δίσκος (discos), in reference to the disc-like hypanthium base remaining after the capsule has dehisced.

1. *Discaria pubescens* (Brongn.) Druce

Bot. Soc. Exch. Club Brit. Isles Rep. 1916, *Suppl.* 2: 620 (1917). — *Colletia pubescens* Brongn., *Mém. Fam. Rhamnées* 59 (1826). — *Discaria australis* Hook., *Bot. Misc.* 1: 157, t. 45 (1829), *nom. illeg.* — *Discaria pubescens* (Brongn.) Domin, *Biblioth. Bot.* 89: 919 (1927), isonym. — **Type citation:** "Novâ Hollandiâ, ad Cox flumen, ad septentrionem Bathurstii. (V. in herb Hooker.)". **Holotype:** "Genus allied to Colletia, Cox' River, Macquarie do + Country North of Bathurst", [*A. Cunningham 70 (10th despatch)*] (multi-sheet type: K000356670, ex Herb. Hook., annotated by M.C. Johnston as "Holotype"; K00356707, specimen in middle and on the left, ex Herb Hook., annotated "Colletia pubescens Brongn. – from thi[s] his description was made W. J. H.[ooker]"; Fig. 2). **Possible isotypes:** Cox's River, New South Wales, Oct. 1822, *A. Cunningham 70 (10th despatch)* (K000356667, photo seen, donated to K by R. Heward in 1862; cited as "holótipo" by Tortosa, *Bol. Soc. Argent. Bot.* 22: 317 (1983), as "Kew Negative 13460"); "specm. with leaves (Oct. 1822 list)", *A. Cunningham 70 (10th despatch)* (MEL56191).

Solenantha spinosa G.Don, *Gen. Hist.* 2: 39 (1832). — *Cryptandra spinosa* G.Don, *Gen. Hist.* 2: 39 (1832), *nom. inval.*, *pro syn.* — *Cryptandra spinosa* (G.Don.) Steudel, *Nomencl. Bot. ed. 2*, 1: 449 (1840). — **Type citation:** "Native of New Holland, on rocky hills, Cox's River." **Lectotype (here designated):** "Genus allied to Colletia, Cox' River, Macquarie do + Country North of Bathurst", [*A. Cunningham 70 (10th despatch)*] (multi-sheet type: K000356670 & K00356707).

Tetrapasma juncea G.Don, *Gen. Hist.* 2: 40 (1832). — *Tetrasperma juncea* Steudel, *Nomencl. Bot. ed. 2*, 2: 673 (1841), *orth. var.* (in error for *Tetrapasma*). — *Tetraspora juncea* Hook., *Fl. Tasman.* 1: 69 (1855), *orth. var.* (in error for *Tetrapasma*). — **Type citation:** "Native of New Holland, at Cox's River, Bathurst, and on the banks of the Macquarie." **Lectotype (here designated):** "specm. with leaves (Oct. 1822 list)", *A. Cunningham 70 (10th despatch)* (MEL56191). **Isolectotype:** Cox's River, New South Wales, Oct. 1822, *A. Cunningham 70 (10th despatch)* (K000356667, photo seen, donated to K by R. Heward in 1862).

Colletia cunninghamii Fenzl in Endl. *et al.*, *Enum. Pl.* 23 (1837). — **Type citation:** "New South Wales, in collibus ad Hunters River, (Cunningham.)". **Lectotype (here designated) or perhaps holotype:** New South Wales ad Hunters River, *A. Cunningham s.n.* (W0002220, photo seen, left hand specimen).

Pomaderris oxyphylla Fenzl in Endl. *et al.*, *Enum. Pl.* 23 (1837), *nom. inval.*, *pro syn.*

Semideciduous *shrub* 0.3–2.4 m high, with glabrous or sparsely pubescent young stems; spines (15–) 25–70 mm long. *Leaves* caducous, concolorous or distinctly discolorous; stipules 0.8–2 mm long; petiole 0.5–2 mm long; lamina ovate, oblong to obovate, 3–6.5 (–12) mm long, 1–2.6 (–5.5) mm wide, base narrowly cuneate to cuneate, entire or serrulate, apex emarginate, apiculate or tridentate, venation obscure. *Inflorescence* of up to 50 flowers; bracts persistent, 0.5–0.7 mm long. *Pedicels* 2–5 (–7.5) mm long. *Hypanthium* tube 0.5–0.8 mm long, 1.8–2.7 mm diameter. *Sepals* 1.1–1.6 mm long. *Petals* 0.7–1.2 mm long. *Stamens* 0.6–1.1 mm long. *Disc* lining the base of the hypanthium tube around the ovary, slightly sinuate. *Style* 0.5–1 mm long, entire (rarely minutely lobed). *Fruit* 2.6–4 mm long. *Seed* 2.2–3 mm long. **Fig. 1A–C.**

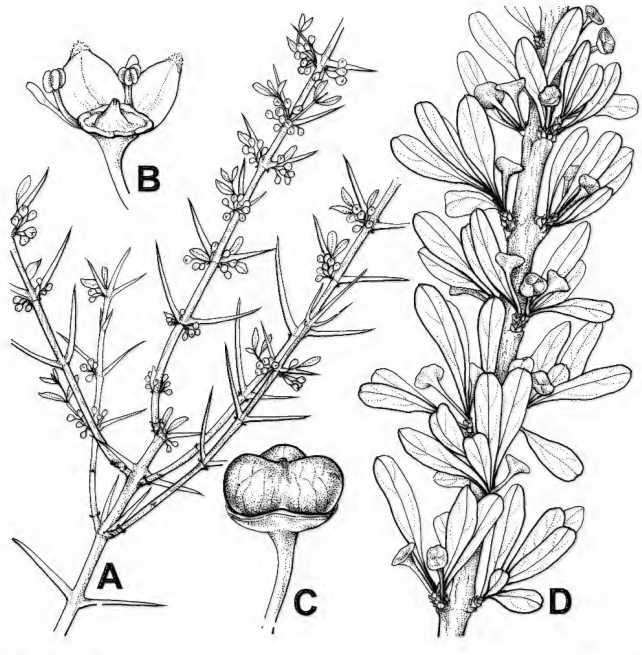

Fig. 1. A–C *Discaria pubescens*: **A** flowering branch ×0.5. **B** half flower ×6. **C** fruit ×3. **D** *Discaria nitida*, branch with remnant pedicels, after fruits have fallen ×1. — A *A.C. Beauglehole 34884* (MEL0544194), B *J.H. Willis s.n.* (MEL2254026), C *D. Parkes EG 93* (MEL1543486), D *A.N. Rodd 5359* (MEL1581796). Illustration by Mali Moir, first published in *Flora of Victoria* 4: 84, Fig. 14 (1999). Reproduced with permission from the Royal Botanic Gardens Victoria.

Illustrations: W.R. Hooker, *Bot. Misc.* 1: pl. 45 (1829), flower only, as *D. australis*; R.D. Tortosa, *Bol. Soc. Argent. Bot.* 22: 330, fig. 7A–C (1983); T.D. Stanley & E.M. Ross, *Fl. south-eastern Queensl.* 2: 49, fig. 6D (1986); N.T. Burbidge & M. Gray, *Fl. A.C.T.* 253, fig. 250 (1970); G.J. Harden, *Fl. New S. Wales.* 1: 373 (1990); F. Coates, *Conserv. Ecol. Managem. Five Rare Spp. Rhamnaceae* 68, fig. 9.1 (1991); N.G. Walsh *in* N.G. Walsh & T.J. Entwistle, *Fl. Victoria* 4: 84, fig. 14a (1999).

Nomenclatural history. Cunningham (1825) first described specimens of *D. pubescens* from plants he collected in Oct.–Dec. 1822 between Sydney and Bathurst. But he assumed that he dealt with two taxa, namely "80. Rhamneae. A genus related to *Colletia*" and "81. Rhamneae. Another genus of this order related to *Colletia*". He based his no. 80 on specimens with 5-merous flowers and leaves, whereas no. 81 had 4-merous flowers and was leafless, i.e. only had spiny green stems. Specimens of *D. pubescens* from this collecting trip were sent to Kew as no. 70 in his 10th despatch of specimens (Orchard & Orchard 2020). While Cunningham used his 1822 collection for the publication, he certainly would have also had access to specimens collected a few years earlier from the Macquarie River, in 1817, which were sent to Kew as no. 389 (2nd despatch). Both lots of specimens were also accompanied by annotated lists, in which he described the specimens (Tab. 1).

Brongniart visited Britain during the completion of his *Mémoire sur la famille des Rhamnées* to examine original specimens in the herbaria of Banks, Lambert and Hooker. He describes *Colletia pubescens* from material in Hooker's herbarium, who then resided in Glasgow, stating that leaves are rarely present and that the species has both, 4- and 5-merous flowers (Brongniart 1826; Tab. 1). It is curious that he did not seem to have examined material of the species collected by Robert Brown in Tasmania, which would have been present in Banks' herbarium.

Hooker (1829) erected the genus *Discaria* and published the illegitimate name *D. australis* for the same species, not using Brongniart's epithet, because he thought that "the name *pubescens* is scarcely applicable, for in general, the stems, branches, and thorns are quite glabrous" (Hooker 1829: 157). This name was in use until the early 20th century, when Druce (1917) finally transferred *Colletia pubescens* to *Discaria*, using the correct epithet.

Table 1. Comparison of the publications of Cunningham, Brongniart, Hooker and Don on *Discaria pubescens* with Cunningham's notes accompanying his collections. Extracts from Cunningham's annotated list of specimens sent to Joseph Banks and W.T. Aiton from Orchard & Orchard (2020).

Cunningham's Lists	**Cunningham (1825)**	**Brongniart (1826)**	**Hooker (1829)**	**Don (1832)**	
10th despatch, no. 70 [1822 collection]. Rhamneae related to Colletia. Perianthium monophyllum quadrifidum. Cor. 0, squamae 4 cucullatis inter segmenta perianthia. Antherae 2-locularis subsingulis squamis, stigma 3-lobatum 3-loculare. An erect shrubby plant (at this season) without leaves, with brachiate strong thorns beneath which preceeds clusters of flowers, Cox' River, 9 Oct., Macquarie River and Country north of Bathurst, Dec.	80. Rhamneæ. A genus related to *Colletia*. *Calyx* quinquefidus persistans. *Corolla* 5-petala in tubum conniventia decidus. *Antheræ* 5, biloculares subsingulis squamis insertæ. *Germen* bilobum. *Frutex* rigidus ramosus spinescens, folia oblongo-lanceolata pauci serrata sparsa et fasciculata, flores axillares et laterales. Rocky hills. Cox's River.	COLLETIA. Kunth. – Colletiae spec. Vent. Decand. […] 4. Colletia pubescens, ramis subaphyllis, pubescentibus; ramulis simplicibus, spinescentibus; foliis raris, oppositis, obovatis, minutis, integerrimis, pubescentibus. Flores axillares, racemose; racemis brevibus, multifloris, infra spinas nascentibus. Calyx urceolato-campanulatus, 4–5-fidus. Petala parva, linearia, convolute; Antherae ovatae, bioculares. Discus cupularis, margine integro. Stylus brevis. Hab. In Nová Hollandiâ, ad Cox flumen, ad septentrionem Bathurstii. (V. in herb. Hooker.)	DISCARIA […] *Calyx* brevi-campanulatus, 4–5 fidus, coloratus. *Petala* 4–5 staminibus minora. *Antherae* biloculares, longitudinalite dehiscentes. *Discus* basin germinis cingens, pateriformis, carnosus, margine angusto elevato, libero, subintegro. *Germen* superum. *Stylus* brevis. *Stigma* trilobum. […] To this genus must unquestionably be referred the *Colletia pubescens* * of Brongniart […]. * This plant, a native of Cox's Rivert at Bathurst, and the banks of the Macquarie, New Holland, is described by Mr. Allan Cunningham […] in Mr. Barron Field's Memoirs on New South Wales, p. 352, n.fl., as "a second new genus of the order *Rhamneae*, and related to *Colletia*". […] Discaria *australis*; calyce 4-fido, segmentis erectis.	XXI. SOLENANTHA […] Calyx permanent, 5-cleft. Petals 5, conniving into a tube, deciduous. Disk? Anthers 5, 2-celled, each inserted under a scale. Ovary 2-lobed. – A stiff-branched spiny shrub with oblong-lanceolate, somewhat serrated leaves, scattered and in fascicles. Flowers axillary and lateral, white. 1 S. spinosa. ħ. G. Native of New Holland, on rocky hills, Cox's River. *Spiny* Solenantha. Fl. Ap. Ju. Clt. 1826. Shrub 1 to 2 feet.	XIII. DISCARIA […] Calyx short, campanulate, 4-5-cleft, coloured. Petals 4–5, smaller than the stamens. Anthers 2-celled, bursting lengthwise. Disk girding the base of the germ, bowl-shaped, fleshy with narrow, elevated, nearly entire, free margins. Ovary half superior. Style short, crowned by a 3-lobed stigma. – Spiny shrubs. […] 2. D. Australis […] calyx 4-cleft, with erect segments. ħ. G. Native of New Holland at Cox's River to the south of Bathurst.
2nd despatch, no. 389 [1817 collection]. Frutex rigida, spinis oppositis. Gullies and rocky descent near Macquarie River, 27 Aug[t].	81. Rhamneæ. Another genus of this order related to *Colletia*. *Calyx* s. *Perianthium* monophyllum quadrifidum. *Corolla* o. s. squamæ 4-cucullatæ inter segmenta perianthii. *Antheræ* 2-loculares, sub singulis squamis. *Stigma* 3-lobatum. *Germen* 3-loculare. A junceous shrubby plant, with brachiate strong thorns. Cox's River. Bathurst—on the banks of the Macquarie.			XXII. TETRAPASMA […] Calyx 4-cleft. Petals 4, cucullate, inserted within the petals. Stigma 3-lobed. Ovary 3-celled. – A rushy, shrubby plant, with brachiate strong thorns. 1 juncea. ħ. G. Native of New Holland, at Cox's River, Bathurst, and on the banks of the Macquarie. Flowers probably white. *Rushy* Tetrapasma. Shrub.	

Domin (1927) republished that combination, because he was apparently unaware of Druce's paper.

In addition to accepting *Discaria* and the species *D. australis* (i.e. *D. pubescens*), George Don (1832) also created two new genera for Cunningham's (1825) taxa, describing no. 80 as *Solenantha spinosa* and no. 81 as *Tetrapasma juncea*. Don does not seem to have examined specimens, he only recycled Cunningham's written Latin descriptions and translated them into English. However, all three species, *Discaria australis*, *Solenantha spinosa* and *Tetrapasma juncea* are based on the same specimens (Tab. 1).

While Brongniart and Don do not mention the collector, it is very clear after examining Hooker's herbarium at K, that specimens from north of Bathurst and the Cox and Macquarie Rivers were collected by Cunningham.

Cryptandra spinosa is a name that was first mentioned by Don (1832) in synonymy with *Solenantha spinosa* and attributed to Cunningham. However, Cunningham never published that name and it is an invention of Don that was later also republished by Steudel (1840). The name *Tetrapasma* was mis-spelt as *Tetrasperma* and *Tetraspora* by Steudel (1840) and Hooker (1855), respectively.

***Typification of* Colletia pubescens.** The type at K was cut into two halves, which were then mounted on separate sheets: the left half of the sheet (Fig. 2A) contains one branch with an original label in Cunningham's hand (branch A1: K000356670), a pencil drawing by Hooker of the flower is also attached; the right half of the sheet (Fig. 2B) contains three branches: the left and middle branch (B1 and B2) are very similar and belong to one collection without collection details (K000356707), the right branch (B3) is of a later collection from Tasmania (K000356708).

When the two halves of the sheets are united (Fig. 2C), then it becomes clear that the three branches A1, B1 and B2 are very similar and seem to belong to one gathering, whereas branch B3, with its own label, is slightly different: it has more leaves and very densely packed flowers, which are a slightly lighter colour. Assuming that branches A1, B1 and B2 are from the same gathering, then the absence of a label and collecting information for branches B1 and B2 also makes sense.

The collecting information is on Cunningham's handwritten label attached to branch A1, namely "Cox' River, Macquarie do + Country North of Bathurst". This is the same information given in Brongniart's account of *Colletia pubescens*, in particular the statement "north of Bathurst" ("ad septentrionem Bathurstii"; Brongniart 1826, see also Table 1) is not repeated on any other label.

McNeill (2014) and Mosyakin *et al.* (2019) discuss the typification of names that were published before the adoption of the type-method. Names published before 1958 did not require that a type specimen was indicated in the protologue, and usually all gatherings cited by the author, and any duplicates of these gatherings, are regarded to be syntypes and isosyntypes. However, when it can be shown that an author only used one particular specimen "when preparing the account of a new taxon" then this specimen can be seen to be the holotype (Art. 9.1. & Art. 9 Note 1; Turland *et al.* 2018; see also Turland *et al.* 2020), in particular, if the author stated that he examined a gathering from one particular herbarium, and if there is only one specimen of that gathering present in that herbarium (Mosyakin *et al.* 2019).

We regard the combined sheet (Fig. 2C) to be a rare example of a pre-1958 holotype, for the following reasons:

- Brongniart (1826) stated in the protologue that he described the species from material in "Herb. Hooker". Hooker (1829: 151) reiterated this and stated that Brongniart described "*C. pubescens*, a New Holland one [i.e. species] from my Herbarium".

  Later, when Hooker's herbarium was incorporated into the K collection in 1867, all specimens received a circular "Herbarium Hookerianum" stamp and can so be identified (Orchard & Orchard 2013). The branches on the combined holotype specimens have such a round stamp, and the original label agrees with the location given in the protologue.

- The combined holotype sheet is annotated in the bottom corner with "Colletia pubescens Brogn. – from thi[s] his description was made" with the cut-off and barely legible initials "W.J.H.", i.e. W.J. Hooker indicated that this was the very sheet that Brongniart examined when drafting the description of *Colletia pubescens*.

  The detailed pencil drawing of the flower has the note "mostly only 5 lobes" in Hooker's hand, which is consistent with the description by Brongniart (1826) of the flowers being 4–5-merous.

- Orchard & Orchard (2020) identified K000356670 and K00356707 to be part of the gathering *A. Cunningham 70*, which was sent by Cunningham to London in his 10th despatch of specimens in March 1823. The only other sheet of the species in Hooker's herbarium is annotated "Frutex rigida, M.R. [Macquarie River]", i.e. has a different location than given in the protologue, and is from another gathering, namely *A. Cunningham 389 (2nd despatch)* (Orchard & Orchard 2020). Hence the combined type sheet is the only type specimen in the Hooker Herbarium.

  Cunningham's collections were sent to Hooker in Glasgow by his brother Richard Cunningham (London) and also by Charles Telfair. For example, specimens from north of Bathurst were sent to Hooker on 22 Oct. 1824, others from around Sydney later on (Orchard 2014). This means

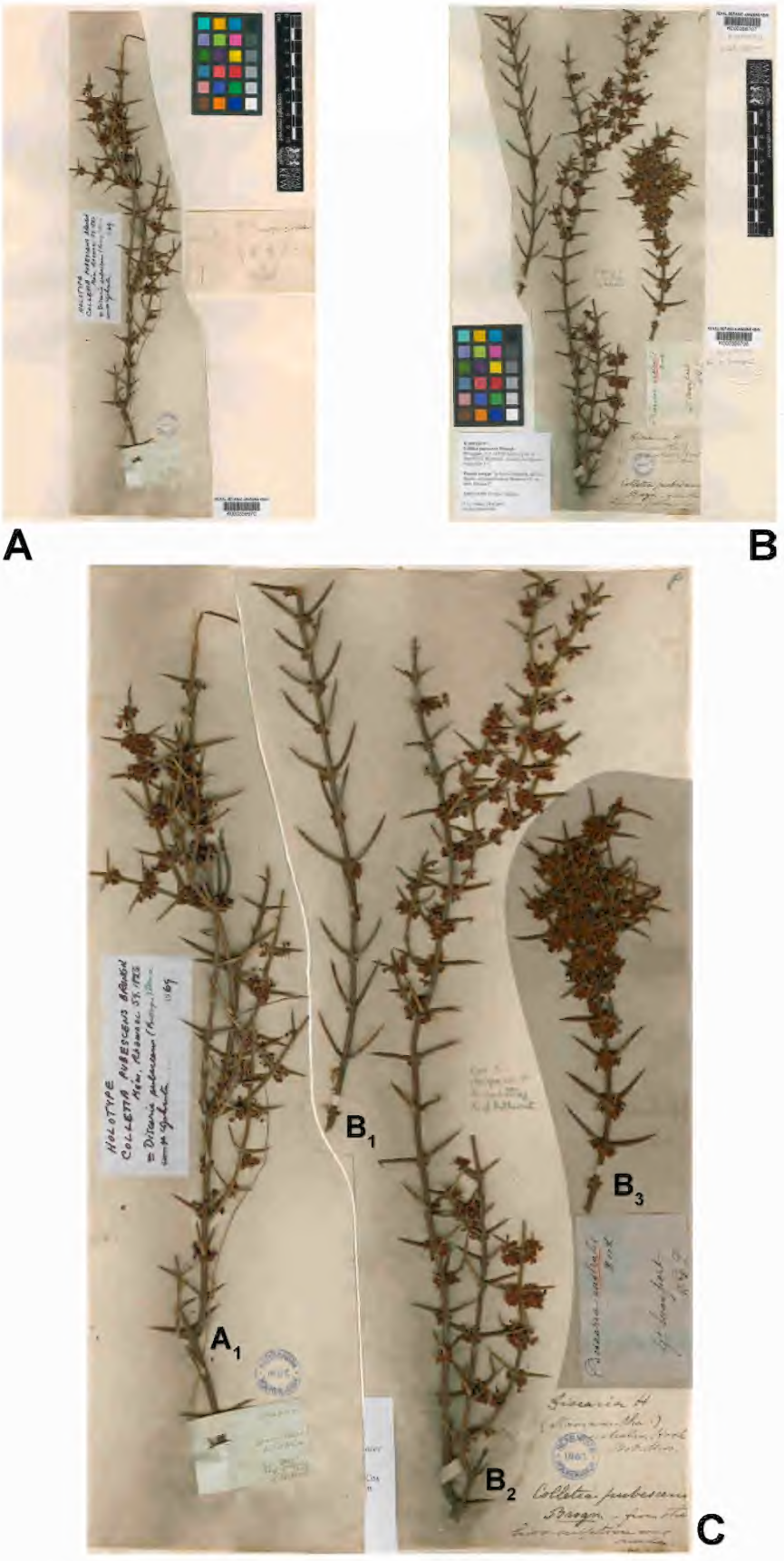

Fig. 2. Holotype of *Colletia pubescens* Brongn., collected by Allan Cunningham and stored in the Hooker Herbarium at the Royal Botanic Gardens, Kew. **A** Sheet with the left hand part of the type (K000356670), with field collecting label around stem: "Genus allied to Colletia, Cox' River, Macquarie do + Country North of Bathurst". **B** Sheet containing the right hand part of the type (K00356707) and an unrelated specimen (K00356708), labelled at bottom of sheet with: "Colletia pubescens Brongn. – from thi[s] his description was made W. J. H.[ooker]". **C** Composite image, combining the two type sheets along the cutting line; the holotype collection consists of branches A_1, B_1 and B_2. The unrelated specimen B_3 which was not collected by Cunningham is shaded. — Images copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

that specimens from that location were present in Hooker's herbarium when Brongniart visited him, presumably either late in 1825 or early in 1826.

As the holotype was later cut and mounted on two sheets (K000356670 & K00356707; Fig. 2), both sheets are part of the type collection, i.e. it is a multi-sheet type (Art. 8.3; Turland *et al.* 2018).

Specimens labelled as *Cunningham 70* are accepted as possible isotypes, but a *Cunningham 70* collection from "South of Bathurst" is not regarded to be type material, as the location does not agree with the protologue. Specimens without collecting number or date are also excluded from the type series (see below).

Tortosa (1983b) stated in error that he had seen "una fotografía del holótipo: New South Wales, Cox's River, A Cunningham 70, Oct. 1822 (Kew negative nº 13460)" (the collection now has the barcode K000356667). As there is a holotype for the name *Colletia pubescens*, this does not constitute inadvertent lectotypification (according to Art. 9.10; Turland *et al.* 2018). Tortosa was simply not sent photographs of all Cunningham collections at K and assumed that the specimen was the holotype, but in fact, it is one of the possible isotype specimens of the name. That collection was donated to Kew by Robert Heward in 1862 from the estate of Allan Cunningham, i.e. it was from Cunningham's own herbarium (Orchard 2014) and not present in Hooker's herbarium when Brongniart examined specimens.

***Notes on* Solenantha spinosa *and* Tetrapasma juncea.** Don (1832) cites "Cryptándra spinòsa, Cuning. In Field's new south wales, p. 352" in synonymy of his *Solenantha spinosa*. However, Cunningham (1825) only lists the taxon [his no. 80] as "A genus related to *Colletia*". For *Tetrapasma juncea*, Don does not cite any previously published names in synonymy, even though Cunningham (1825) described a second taxon [his no. 81] as "Another genus of this order related to *Colletia*". Comparing the two publications (Tab. 1), it is clear that Don (1832) simply translated the Latin descriptions of Cunningham (1825): both species are based on Cunningham's collections from 1822, which he used to prepare his enumeration of plants from the Blue Mountains. This means that the specimens of *Cunningham 70 (10th collection)* are syntypes of these two names.

A specimen at MEL that has only 4-merous flowers is designated as lectotype of *Tetrapasma juncea*; an isolectotype at K also seems to have mainly 4-merous flowers, but we could not examine the actual specimen, only photographs. According to the protologue, *Solenantha spinosa* has 5 sepals and petals: the specimen of *Cunningham 70* that has mostly 5-merous flowers is the combined type-sheet mentioned above (Fig. 2), i.e. also the holotype of *Discaria pubescens*. This specimen is here designated as lectotype of *Solenantha spinosa*.

***Notes on* Colletia cunninghamii *and* Pomaderris oxyphylla.** Fenzl's *Colletia cunninghamii* was described from a Cunningham collection from Hunter's River, which is preserved at W. The only specimen found that was annotated with that name is accepted as holotype, but, since Cunningham collections are available in many herbaria and it is possible that a duplicate is extant elsewhere, the advice of McNeill (2014) is followed here and this specimen is simultaneously designated as lectotype. As Cunningham had not explored the Hunter River in New South Wales in the period covered by Orchard & Orchard (2020), the specimen is probably from his 1825 expedition (A.E. Orchard, pers. comm.).

When describing *Colletia cunninghamii*, Fenzl (1837) also cites the name "*Pomaderris oxyphylla* Cunningham msc." in synonymy, but this must have been done in error. It seems that the synonyms of *C. cunninghamii* and the following species, *Cryptandra buxifolia* Fenzl [now *Spyridium buxifolium* (Fenzl) K.R.Thiele], have been mixed up. All specimens seen that were annotated by Cunningham with his manuscript name *P. oxyphylla* are of *Spyridium buxifolium*, which is the next species treated by Fenzl in his overview of Australian Rhamnaceae. The synonym mentioned under *Cryptandra buxifolia*, however, is "*Discaria australis* Cunningh. msc. non Hook."; this would be the correct synonym for *C. cunninghamii*.

Distribution & habitat. Occurs on the Central Plateau and Midlands (Tas.), Ballarat district and eastern ranges (Vic.), N.S.W. tablelands to the Darling Downs district of southern Qld; in heathland, shrubland, or woodland, often in shallow rocky soils derived from granite, limestone or basalt, at 450–1450 m altitude.

Phenology. Flowers (Aug.–) Oct.–Jan.; fruits Oct.–Mar.

Conservation status. The species is listed as 'near threatened' in Queensland (*Nature Conservation Act 1992*) and as 'endangered' in Victoria (*Flora and Fauna Guarantee Act 1988*; Humphries 2003) and Tasmania (*Threatened Species Protection Act 1995*; TSS 2012).

Common name. Australian anchor plant.

Specimens examined *(c. 160 seen)*

QUEENSLAND. 7.7 km along Branch Road, nr Maryvale, alt. 550 m, 4 Oct. 1996, *A.R. Bean 10835* (BRI, HO, MEL, NSW); Property of H. Hall, Swan Ck Road, E of Warwick, alt. 625 m, 5 Oct. 1996, *A.R. Bean 10946* (MEL; CANB, NSW, BRI, *n.v.*).

NEW SOUTH WALES. Apsley R., East Lynne Road, SE of Walcha, alt. 1015 m, 25 Dec. 2006, *A.R. Bean 25920* (NSW); Mt Kaputar National Park (N.P.), The Govenor Lookout, alt. 1432 m, 16 Nov. 2000, *J.J. Bruhl 1978 & I.R. Telford* (AD, NSW; CANB, NE, *n.v.*); Moredur Ck, 20.3 km SE of Jingha P.O., 13 Dec. 1986, *R. Coveny 12388, W. Bishop & L. Murray* (HO, MEL, NSW); Track to Clarke Gorge, Cave Ck, Coolamon Caves area, 44 km NNE of Kiandra, alt. 1180 m, 26 Jan. 1997, *P.C. Jobson 4588* (MEL; NSW, *n.v.*); c. 50 m west of ANU Lodge building, Siding Spring

Anglo-Australian Observatory, alt. 1130 m, 17 Dec. 2007, *R.L. Johnstone 2324* (AD, NSW); c. 300 m downstream from Snowy Mtns Hwy bridge along Yarrangobilly R. (at bend in river), at Yarrangobilly Village, 24 Feb. 2009, *A.E. Orme 682* (NSW; CANB, *n.v.*); Kosciuszko N.P., first creek crossing below Blue Waterhole along tk to Clarkes Gorge, alt. 1190 m, 11 Dec. 2013, *N.G. Walsh 8065* (MEL).

AUSTRALIAN CAPITAL TERRITORY. Brindabella Ra., between Uriarra and Piccadilly Circus on Brindabella Road, 20 Nov. 1956, *H. Eichler 13278* (AD).

VICTORIA. 0.5 miles NW of junction of Benambra–Snowy River Road at Wulgulmerang, 7 Jan. 1970, *A.C. Beauglehole 33350* (MEL; NSW, *n.v.*); Cobungra, 1 km S of road and beside Victoria R., 19 Nov. 1973, *D.J. McGillivray 3191* (MEL, NSW); Alpine N.P., Snowy Ra., 10 m NE from the junction of Guys Hut Tk and Piemans Falls Tk, alt. 1430 m, 12 Feb. 2006, *V. Stajsic 4967* (MEL); MacFarlane Flat, on the true right bank of main ck flowing NW to Berrima R[iver], near NW end of open grassy plain, alt. 1000 m, 29 Dec. 1998, *R. Thomas 748* (MEL); Limestone Ck, Caves area c. 2.2 km due N from junction of Limestone Ck Track with Limestone Road (Black Mtn Road), alt. 960 m, 30 Nov. 1989, *N.G. Walsh 2866* (MEL).

TASMANIA. Waddamana Road, 12 Dec. 2003, *B. French s.n.* (HO539688); Grassy Hut Ck, S of Bothwell, 10 Nov. 1991, *L. Gilfedder 57* (HO); Shannon R., escarpment on S bank, 20 Dec. 1998, *A.M. Gray 856* (HO); 3 km S of Perth above the banks of the South Esk R., 14 Dec. 2001, *A.J. North & I. Riley s.n.* (HO522950); Bashan Road verges from 100 m S of Ouse River bridge for 3.6 km, 6 Mar. 2009, *M. Visoiu, J. Wood & N. Gill 610* (HO); Fordell Ck, NW of Bothwell, 13 July 2011, *M. Wapstra 1267* (HO).

Other Cunningham collections

Specimens listed as "*n.v.*" are reported in Orchard & Orchard (2020).

NEW SOUTH WALES. Macquarie R., 1817, *A. Cunningham 389 (2nd despatch)* (BM *n.v.*); Macquarie R., New South Wales, Aug. 1817, *A. Cunningham 389 (2nd despatch)* (K000356668, photo seen, donated to K by R. Heward in 1862; cited as "síntipo" by Tortosa, *Bol. Soc. Argent. Bot.* 22: 317 (1983), as "Kew Negative 13460"); Macquarie R., N.S.Wales, Aug. 1817, *A. Cunningham 389 (2nd despatch)* (MEL56184, sterile, annotated by Tortosa as "Isotypus a D. australis Hook"); "South of Bathurst, Colony", 1822, *A. Cunningham 70 (10th despatch)* (BM *n.v.*); "in the rocky bed of rivers", N.S. Wales, Apr. [*sic*] 1817, *A. Cunningham s.n.* (CGE *n.v.*, ex Herb. Lindley; the month "Apr." most likely a transcription error); "Frutex rigida, M.R. [Macquarie River]", *A. Cunningham s.n.* (K *n.v.*, ex Herb. Hook.); New South Wales, *A. Cunningham s.n.* (P06887642, photo seen, ex MEL with a blue "Phytologic Museum of Melbourne" label; possibly separated from MEL56184 or MEL56191 and sent to Paris, labelled as "Reçu de 26 juillet 1906"); "147. Trevoa like", "N[elle]. Hollande, Voyage de la Vénus, 1839", *A. Cunningham s.n.* (P06887638, photo seen, ex Herb. Petit-Thouars).

2. *Discaria nitida* Tortosa

Hickenia 1: 109 (1977). — **Type citation:** "Australia: Victoria. Cobungra, about 3,000 ft. alt. (10 feet high, trunk 3" in diam.) H.B. Williamson, XII-1928 (MEL 56204)." **Holotype:** Spring Creek, Cobungra, "spineless form / ten feet high / trunk 3" in diam.", Dec. 1928, *H.B. Williamson s.n.* (MEL56204). **Isotypes:** BAA00004337 (photo seen, labelled as "clastotipo ex MEL"); MEL0236591 (formerly in Ref. Herb.); NSW 721829, *n.v.* **Possible Isotypes:** Spring Creek, Cobungra, "tall form / 10ft high stem / 6 ½ inches in circum.", *H.B. Williamson s.n.* (MEL2103601); Cobungra, Dec. 1928, *H.B. Williamson s.n.* (MEL2103602).

Discaria pubescens auct. non (Brongn.) Druce: J.H.Willis, *Victorian Naturalist* 72: 51 (1955).

Evergreen or semideciduous *shrub*, 2.5–3 m high, with sparsely pubescent young stems; spines 5–15 (–18) mm long, rarely absent. *Leaves* persistent, ± concolorous; stipules 1–1.5 mm long; petiole 0.5–3.5 mm long; lamina narrowly obovate to obovate, (5–) 9–17 mm long, 2.2–5 (–7.3) mm wide; base narrowly cuneate; entire or serrulate; apex obtuse, emarginate or apiculate; venation clear (at least below). *Inflorescence* of up to 10 flowers; bracts persistent, c. 1.5 mm long. *Pedicels* 2.4–4 mm long. *Hypanthium* tube 1–1.1 mm long, 2–2.5 mm diameter. *Sepals* 1.4–2 mm long. *Petals* absent. *Stamens* 0.8–1.3 mm long. *Disc* forming a wide ring around the ovary, deeply scalloped between the staminal bases. *Style* 1–1.2 mm long, branched. *Fruit* 3–3.5 mm long. *Seed* 2.7–3 mm long. **Fig. 1D.**

Illustrations: R.D. Tortosa, *Hickenia* 1: 111, fig. 1 (1977); R.D. Tortosa, *Bol. Soc. Argent. Bot.* 22: 330, fig. 7G–I (1983); G.J. Harden, *Fl. New S. Wales.* 1: 373 (1990); N.G. Walsh *in* N.G. Walsh & T.J. Entwistle, *Fl. Victoria* 4: 84, fig. 14b (1999).

Distribution & habitat. Occurs from Cooleman Caves (N.S.W.) to Cobungra (Vic.); usually along watercourses in sandy or rocky soils, often in woodlands, particularly of black sallee (*Eucalyptus stellulata* Sieber ex DC.) or snow gum (*Eucalyptus pauciflora* Sieber ex Spreng.), at 915–1200 m altitude.

Phenology. Flowers Nov.–Jan.; fruits Jan.–Apr.

Conservation status. The species is listed as 'vulnerable' in New South Wales (*Biodiversity Conservation Act 2016*) and as 'endangered' in Victoria (*Flora and Fauna Guarantee Act 1988*).

Common name. Leafy anchor plant.

Specimens examined

NEW SOUTH WALES. Blue Waterholes, Cooleman Caves area, 44 km NNE of Kiandra, alt. 1180 m, 26 Jan. 1997, *P.C. Jobson 4586* (NSW; CANB, MEL, *n.v.*); c. 350 m downstream from Snowy Mtns Hwy bridge along Yarrangobilly R., at Yarrangobilly Village, 24 Feb. 2009, *A.E. Orme 678* (NSW; CANB, MEL, *n.v.*); Alpine Ck fire Trail at Tantangara Ck crossing, approx. 9.4 km N of Snowy Mtns Hwy, alt. 1362 m, 7 Feb. 2017, *G.P. Phillips 274* (NSW); Snowy Mtns Hwy, Alpine Ck crossing, 14.2 km SE of Kiandra, *A.N. Rodd 5359* (MEL, NSW; PRC, *n.v.*); Kosciuszko N.P., Gulf Plain, c. 150 m above Murrumbidgee R., c. 500 m E from Tantangara Dam spillway, alt. 1200 m, 21 Nov. 2002, *N.G. Walsh 5676* (MEL); Thredbo

R., southern bank, c. 4.8 km downstream of Thredbo Alpine Village, 26 Nov. 2015, *G.T. Wright 377* (NSW; CANB, *n.v.*).

VICTORIA. Beside the Victoria R. about 1.5 km downstream from Malcolm Plain, Cobungra area, alt. 1315 m, 18 Feb. 2011, *J.A. Jeanes 2606* (MEL); Spring Ck, Cobungra, Jan. 1929, *H. Morgan 1* (MEL); Rocky sides of the Victoria R., May 2000, *K.C. Norris s.n.* (MEL2109146); Thredbo R., Kosciuszko N.P., 19 Nov. 1998, *G.T. Wright 71* (MEL).

3. *Discaria nitida* × *D. pubescens*

Wright & Briggs (2000) report hybrids between *D. pubescens* and *D. nitida* at several populations in New South Wales where both species occur. Hybrids have also been found in Victoria. They exhibit intermediate characteristics (e.g. in habit, height or leafiness) and usually have some flowers with ruminant petals inserted on or at the base of stamens.

Intra- and intergeneric hybrids are quite well-known in Colletieae and have been reported from South America (Tortosa 1983a, 1988; Medan *et al.* 2012).

Specimens examined

NEW SOUTH WALES. Sawpit, Kosciusko N.P., 17 Dec. 1971, *A.M. Ashby 4437* (AD97304154 & AD97419255); 0.5 km downstream from Blue Waterholes on Cave Ck, alt. 1180 m, 19 Nov. 1997, *J.D. Briggs 2731* (NSW; CANB, *n.v.*); c. 300 m downstream from Snowy Mtns Hwy bridge along Yarrangobilly R. (at bend in river), at Yarrangobilly Village, 24 Feb. 2009, *A.E. Orme 681 & E. Mills* (NSW); Sawpit Ck, approx. 200 m downstream from bridge that crosses Pillabo Tk, 5 Nov. 1998, *G.T. Wright 41 & D.T. Woods* (MEL, NSW, CANB); Yarrangobilly R., 600 m downstream of bridge that crosses Snowy R., alt. 1005 m, 12 Nov. 1998, *G.T. Wright 69* (NSW; CANB, *n.v.*); Unnamed creek, 100 m W of the intersection of Nungar Ck and Alpine Ck fire trails, Boggy Plain, alt. 1360 m, 7 Jan. 2000, *G.T. Wright 141* (NSW; CANB, *n.v.*); Yarrangobilly R., 600 m downstream of bridge that crosses the Snowy Mtns Hwy, alt. 1005 m, 12 Nov. 1998, *G.T. Wright s.n.* (NSW509610).

VICTORIA. Spring Ck, Cobungra, Jan. 1929, *H. Morgan 2* (MEL).

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